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STUDIES ON THE PHYLOGENETIC CLASSIFICATION OF DIPTERA CYCLORRHAPHA,
WITH SPECIAL REFERENCE TO THE STRUCTURE OF THE MALE POSTABDOMEN

by



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The undersigned certify that they have read,
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ABSTRACT

This work presents a review of the classification of the Diptera Cyclorrhapha, based both on information available in the literature and on the results of my own analysis of characters of the male postabdomen and genitalia. The classification proposed is intended to be a phylogenetic classification consisting of probably monophyletic groups. A review of the principles and procedures of biological systematics is included.

The morphology of the male postabdomen and genitalia of the Diptera Cyclorrhapha is discussed. Recent observations on newly emerged Platypezidae provide conclusive evidence that the 8th abdominal segment in Cyclorrhapha is rotated through half the angle of hypopygial rotation, thus becoming inverted (rotated through 180°) when the hypopygium has become circumverted (rotated through 360°). In Platypezidae hypopygial rotation is not completed until after emergence from the puparium and is partly reversed during copulation, which takes place with the hypopygium in the inverse position. I conclude on the basis of comparative morphology that the so-called "epandrium" of the Cyclorrhapha and some Empididae is formed by fusion of the basimeres across the dorsum, and is therefore not homologous with the epandrium of other Diptera (which has been completely lost in all Cyclorrhapha according to this interpretation). The new term periandrium is therefore proposed for the cyclorrhaphous "epandrium".

A review of the classification of the Schizophora leads to a proposed division of the group into five superfamilies: Lonchaeoidea, Lauxanioidea, Drosophiloidea, Nothyboidea and Muscoidea. The prefamily category is introduced between the superfamily and family categories. The Calyptratae

are classified as one of the prefamilies of Muscoidea, which is the largest superfamily of Schizophora. The customary division of the Schizophora into the Calyptratae and "Acalyptratae" is unacceptable in the phylogenetic system, since the latter group is not monophyletic. The new classification proposed is supported by the available ontogenetic evidence, which indicates that the morphological differences between the male postabdomen of Muscoidea and Drosophiloidea rest on differences in the number and development of the imaginal discs.

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1. Introduction

In this work I deal mainly with two interrelated topics, the structure of the male postabdomen and genitalia of cyclorrhaphous flies and how these insects should be classified in a phylogenetic system. New information and interpretation is presented here, as well as commentary on the observations and interpretation of previous authors. The field covered by this work has long been recognized as difficult. I hope that this work will dispel some of the difficulties. My proposal of revised terminology for certain parts of the external genitalia thus should not be regarded as innovation for its own sake, but as an attempt to remedy a situation which has been widely recognized as unsatisfactory.

In proposing a revised classification of the Schizophora, I have followed the type of analytical procedure used by such authors as Crowson and Hennig. In my opinion their rigorous approach to phylogenetic classification provides the best available procedure for constructing a higher classification on logically consistent principles. I discuss this question in detail below (section 2). The importance of a clear understanding of the theory of systematics for the success of attempts at higher classification is worth stressing. The classifications which can be proposed by applying different principles become increasingly divergent as "higher" (more extensive) groups are considered, particularly because of differences in the classification of highly modified forms. Considerations of theory are not irrelevant to the practice of biological systematics as is sometimes maintained. A good contrary example is provided by the history of the classification of the families of Schizophora, for some proposals of different authors have been discordant in the extreme. The classification of the Schizophora provides a good test for the effectiveness of phylogenetic

systematics in dealing with complex patterns of character correlations which older workers were unable to interpret satisfactorily. Hennig (1958) began work on the phylogenetic classification of this group, and my present work continues this endeavour. The classification presented here is still provisional. Many additional studies could be undertaken to test the validity of my proposals, and I hope that publication of this work will stimulate some of my colleagues to undertake such research.

In some parts of this work, I comment critically on the views of other authors. I do this in order to make clear why I have reached different conclusions. Such detailed criticism is in my opinion an important part of every scientific work which has a review content, since without such criticism it is difficult for any reader who lacks a detailed knowledge of the subject to judge whether different conclusions have been reached arbitrarily or with good reason.

I prepared this work at the University of Alberta (Edmonton) during the years 1967 - 1970. I have attempted to consider all relevant literature up to the end of 1969, although I cannot guarantee that nothing has been overlooked in the years since 1965, which have not yet been covered by the "Zoological Record". The material considered in this study may seem small in relation to the field covered, but it should be appreciated that my request lists were already long enough to strain the patience of museum curators. It is particularly regrettable that so little material of South American Diptera could be made available to me, because many of the genera are represented in collections only by a few type specimens. Further studies on the dipterous fauna of this region may be awaited with interest, and I hope that publication of this work will stimulate increased efforts in this field.

The names used in this work for North American species generally follow those in the most recent catalogue (Stone *et al.* 1965), except that for Platypezidae I have followed the revised generic system of Kessel and Maggioncalda (1968a). The names of Palaearctic species generally follow those used in "Die Fliegen der paläarktischen Region". For material from other regions I have used the names under which the specimens were sent to me. While efforts have been made to ensure that there are no errors at generic or higher levels in the identification of specimens figured and described, it is possible that a few identifications may be incorrect at the species level. It was not practicable for me to check all the taxonomic literature on Schizophora, a group containing about five times as many species as the mammals. In most cases species identifications were accepted on trust.

Material and methods

I worked mainly with dried specimens. These were first relaxed in a humidified container, and the abdomen removed with needles under the binocular microscope. Then the abdomen was lightly macerated in potassium hydroxide (about five minutes in a 10% solution at 100° C), and washed for a few minutes successively in (1) tap water, (2) a weak solution of glacial acetic acid (about 20%), and (3) distilled water. After this treatment the preparations were placed on slides without coverslips in a mixture (roughly 50:50) of glycerol and polyvinyl lactophenol. Since the elasticity of chitin is restored and maintained in this medium, I was able to manipulate or further dissect the preparations immediately, whenever the need arose. This constant availability of the preparations for rechecking was essential to the success of the project. The medium did not dry up during the period

of two years during which the preparations were kept in it. At the end of the project I washed off the temporary mounting medium with 50% ethanol in water, and took the preparations through 98% ethanol into neutral Canada balsam for permanent storage (except for some of the preparations of specimens lent by the U.S. National Museum, which were returned in microvials of glycerol). In total, I made preparations of about 220 species during this study: the species of Schizophora concerned are indicated in Appendix 1. In most cases only one or two preparations were made of each species.

I made serial sections of a few specimens fixed in the field in Pampel's fluid. The sections were stained in Gömöri's Chrome Alum haematoxylin and eosin according to standard procedures, and mounted in neutral Canada balsam. I was able to check from these sections the course of the ejaculatory duct and some details of the musculature. The sections will remain in my possession. They represent 21 genera, as indicated in table 1.

2. Principles and procedures of classification

2.1. The representation of phylogenetic relationship in the Linnaean hierarchy

The theory of systematics has been the subject of so much controversy in recent years, that all authors of major systematic works would be well advised to state their theoretical standpoint clearly at the outset and thus prevent possible misunderstanding. Therefore I state that I am concerned in this work with phylogenetic (cladistic) classification, and regard the works of Hennig (1950, 1966a) as important clarifications of the logical foundations of this type of classification. Some of the important features of the theory of phylogenetic systematics, as affecting classification above the species level, will now be outlined in broad terms.

Hennig asserts that all groups in the phylogenetic system should be monophyletic, including descendants of a common ancestral species. This view has of course been held by many leading systematists ever since the acceptance of Darwin's theory of evolution. Hennig's exploration of the implications of this principle leads him to assert that, if ambiguity is to be avoided, groups should only be described as monophyletic if they include *all* the descendants of a common ancestral species (or all descendants in a particular time period, if the systems of different time periods are regarded as separate). This precise definition of the concept of monophyly is necessary if the hierarchical system of classification is to provide unambiguous information on phylogenetic relationships between organisms, that is their recency of common ancestry (whether in absolute or in relative terms). To clarify the grounds for this assertion, I offer the simple hypothetical example shown in figures 1 and 2.

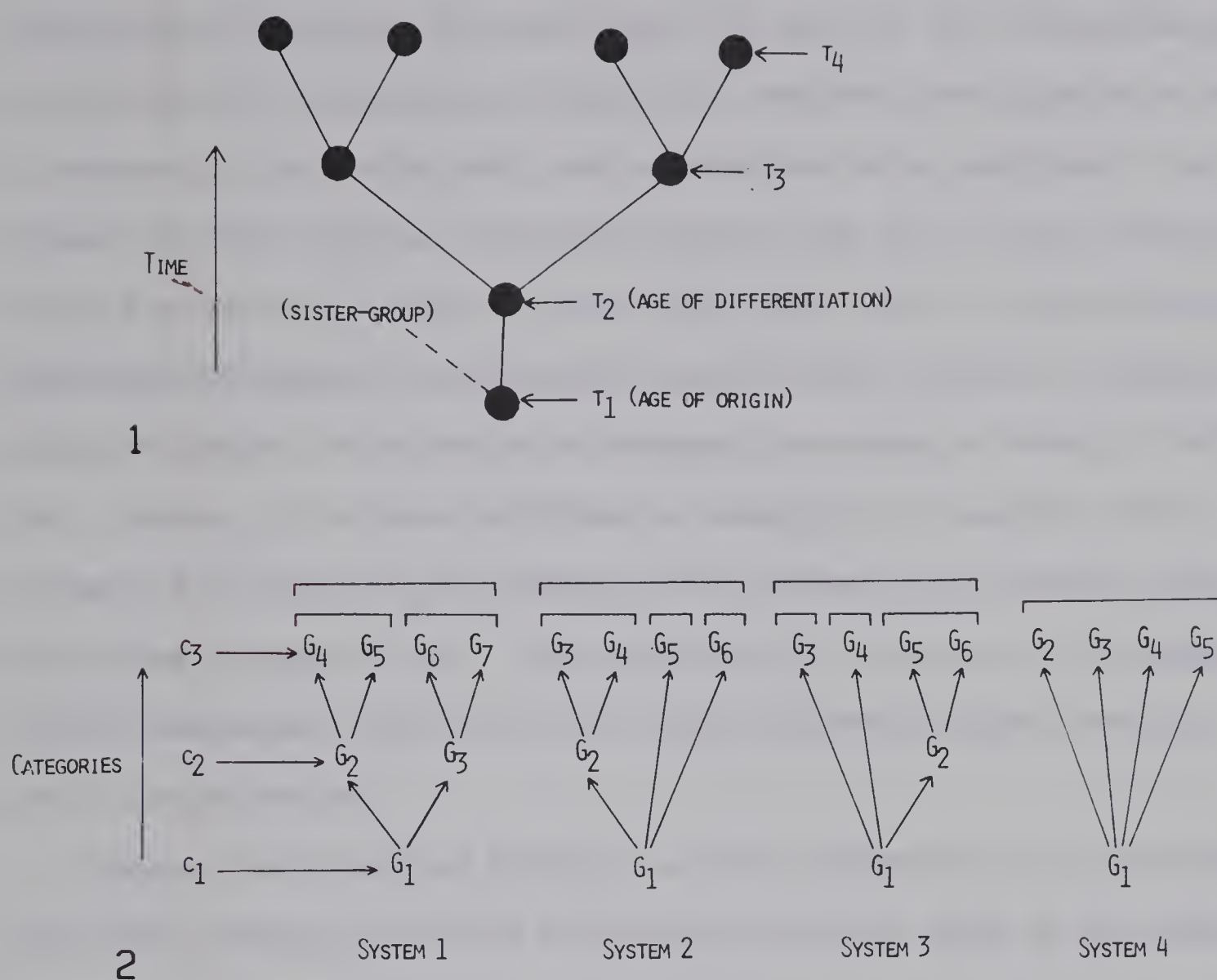


Fig. 1. Phylogeny of a monophyletic group of four species at time t_4 represented by a dendrogram.

Fig. 2. The four possible Linnaean hierarchies which are admissible as representations of the phylogenetic relationships between the four contemporaneous species whose phylogeny is represented by the dendrogram at fig. 1, when all taxa are monophyletic according to Hennig's definition. Two forms of presentation are used, (1) that of Gregg (1954), in which the taxa are numbered ($G_1, G_2 \dots$) and their inclusion relations shown by arrows; and (2) the nesting bracket presentation which is more familiar to systematists. The species (members of category C_3) remain in the same order throughout.

Of the four possible systems shown in figure 2, system 1 obviously conveys more information than the others (in fact all the information about the phylogenetic relationships between the contemporaneous species at time t_4 conveyed by the dendrogram), and is therefore to be preferred. The other systems are less complete, conveying some, but not all, of the information conveyed by system 1. None of these four systems leads to false inferences concerning phylogenetic relationships, and no other systems are possible without violating the criterion of monophyly according to Hennig's definition. However, if a laxer definition of monophyly is accepted, other systems can be admitted (an additional six systems in the example given, thus making a total of ten). The additional six systems are all incongruent with the dendrogram, and thus do not convey information about the phylogenetic relationships.

Simpson (1961) defined monophyly as "the derivation of a taxon through one or more lineages, from one immediately ancestral taxon of the same or lower rank". Authors who follow this definition are faced with few constraints on the delimitation of taxa (see Hull 1964). Since the units of evolution are species, I think that statements about descent are most clearly expressed in terms of descent from (one or more) species. The phrase "derivation from one immediately ancestral taxon of the same or lower rank" in Simpson's definition is to my mind unacceptable, because its meaning in terms of descent from species is not clear. Furthermore, the wording of the definition allows highly heterogenous groups to be accepted as "monophyletic", provided that they are given sufficiently high rank. Simpson used this definition to justify horizontal divisions between taxa in paleontological classification, because of the practical difficulties involved in extending group concepts back in time to the common ancestral species (vertical

classification in paleontology). These difficulties are indeed serious, but I think that the way of resolving them is to restrict the application of the criterion of monophyly, not to redefine the term. The proposals to divide the geological time scale for purposes of classification discussed later in this section provide a possible approach to the problem.

The example above (figs. 1 and 2) illustrates that a Linnaean hierarchy is an adequate representation of the phylogenetic relationships between recent organisms, or organisms in any particular time period. This is one of the grounds for the view of Hennig and other phylogenetic systematists that the phylogenetic system should be expressed by revision of the traditional Linnaean system, rather than by proposal of a separate classification.

Woodger (1952) and Gregg (1954) have studied the definition and properties of hierarchical systems from a logical standpoint. In such systems all the elements are related by unidirectional inclusion relations, emanating ultimately from the "beginner" of the system. The Linnaean hierarchy shows an additional feature which is not present in other hierarchical systems: this is that the taxa (the elements of the hierarchy) are members of categories (such as phylum, class, order, family, etc.), which are associated with the system and indicate a sequence of ranking. A logical distinction should be made between the inclusion relations between taxa, and the membership relations between taxa and categories (Buck and Hull 1966).^{*} Category names are defined in terms of properties which taxa have (Buck and Hull 1966). Clearly some of these properties are formal, involving the use of category names to indicate the sequence of inclusion relations between taxa.

^{*}It is common practice to refer to taxa as "members" of higher taxa, as well as of particular categories. Buck and Hull use the term membership in an unusually restricted sense in the interests of clarity.

Thus when an individual is classified as belonging to the species *Homo sapiens*, the genus *Homo*, the family Hominidae, the order Primates and the class Mammalia, the sequence of inclusion relationships (subordination) between these five taxa is indicated by the reference of the taxa to categories. A definition of a category name may therefore specify the inclusion relations between the taxa referred to this category and taxa referred to at least two other categories. It is possible to maintain that category names have no meaning beyond this formal aspect. But most biologists assume that the taxa referred to a particular category are, or at least ought to be, equivalent to one another not only in a formal sense but also in respect of some of their empirical relations and properties. Considerable controversy has arisen over the nature of these empirical relations and properties which qualify taxa for membership of a particular category. Mayr (1969: 233) summarizes some of the criteria which have been suggested under five headings, as follows: "1. Distinctness (size of gap); 2. Evolutionary role (uniqueness of adaptive zone); 3. Degree of difference; 4. Size of taxon; 5. Equivalence of ranking in related taxa."

However, any attempt at a consistent and precise application of these criteria would be faced with serious difficulties, which I briefly summarize as follows:

1. To speak of gaps in particular character sequences is meaningful, and taxonomists of all schools use such gaps in the normal procedure of defining character states. But to speak of gaps between whole organisms (in other words, the totality of the differences in their attributes) is quite another matter, and any attempt at precise estimation of gaps in this extended sense must lead into a logical and mathematical morass similar to that involved in trying to estimate "overall similarity"

(see section 2.2).

2. An "adaptive zone" is an ecological concept. Since some groups in the phylogenetic system are diverse as regards the ecological roles of their members, it seems scarcely possible to make consistent use of ecological criteria of ranking.
3. The "degree of difference" is a phenetic concept, similar to Mayr's first criterion (size of gap). The extension of such a concept from particular character sequences to whole organisms is likewise problematical (again see section 2.2).
4. Mayr recommends that "the size of the gap justifying the separation of a higher taxon should be inversely correlated to the size of the taxa". The application of a criterion of this kind again depends on estimating gaps between whole organisms.
5. The application of this criterion of equivalence depends on assuming that the related taxa are correctly ranked. This may be an acceptable temporary expedient in studies of a limited range of organisms, but does not provide any general criterion for ranking.

For the reasons given above, I doubt whether the criteria listed by Mayr can be satisfactorily applied to the ranking of taxa in a phylogenetic system in Hennig's sense. Even if the problems of measuring gaps or degrees of difference between organisms could be overcome, a further serious difficulty would arise. This is that the use of such criteria would not necessarily lead to the reference of the monophyletic taxa in a phylogenetic system to categories in a way compatible with the use of the category names to indicate the sequence of subordination. Inconsistencies would need to be admitted in the application either of the criteria for referring taxa to categories, or of the monophyly criterion by which the taxa are delimited (such as by the

admission of paraphyletic groups into the system). The reason for this incompatibility may be shown by comparison of the system of taxa and the phylogenetic relationships between organisms which it represents. If the dendrogram at figure 1 is compared with the complete representation of the phylogenetic relationships in a Linnaean hierarchy (system 1 of fig. 2), the sequence of inclusion relations (subordination) which the categories indicate is clearly congruent with the sequence of branching of the phylogeny in time. Thus the categories necessarily correspond with the time dimension in a relative sense in a system in which all taxa are monophyletic according to Hennig's definition, because the sequence of inclusion relationships (subordination) in such a system is congruent with the branching of the phylogeny in time. It is impossible within the constraints of a phylogenetic system of this kind to define categories in terms of phenetic criteria in a rigorous consistent way, because phenetic divergences and degree of phylogenetic relationship (recency of common ancestry) are not necessarily congruent.

Once it is recognized that the categories in a system of monophyletic groups necessarily indicate the relative age of the stem-species ancestral to members of each taxon, it is but a small step to suggest that categories should be related in broad terms to the absolute age of the stem-species. Hennig (1966a: 186) has made such proposals, and these have been taken up and elaborated by Crowson (1970). To be sure, these proposals have been made a little in advance of their time, since the phylogeny of most groups of organisms (including those treated in this work) has not been sufficiently clarified to allow confident use of a time criterion for ranking. Nevertheless these proposals provide the only theoretically sound basis for achieving an objective equivalence between the taxa assigned to particular categories

in a phylogenetic system, and thus pose a task for future phylogenetic systematics.

The question of which measurement of age is the best reference point for the assignment of taxa to categories thus arises. Hennig has concluded that we should use the age of origin of the stem-species, that is the time at which the stem-species split from its sister-species. A logical consequence of Hennig's conclusion is that sister-groups must have the same rank in the system, because their age of origin is the same. I have indicated the difference between age of origin and age of differentiation on the dendrogram (fig. 1).

The classification of fossil organisms poses certain problems because a Linnaean hierarchy is only an adequate representation of the phylogenetic relationships between Recent organisms, or organisms in any particular time horizon. Brundin (1966) rightly states that "we have to imagine a vast series of horizontal systems upwards through time, together reflecting successive change and the rise and fall of innumerable integrant sister-group systems". Of course such a continuum of systems through time is unmanageable to the human mind, and we have to resort to the device of arbitrarily breaking down the continuum into discrete sections, as Hennig (1950: 259) concluded. The Linnaean systems of different time periods can thus be regarded as different. It is a misconception to think that the demand that all taxa should be monophyletic necessarily leads to an insistence on a "vertical" system in which all taxa are held to extend back in time to include the stem-species and all its descendants. Such vertical groups should be thought of as extensions of taxa into an additional dimension, or series of taxa in the systems of successive time-periods. The Linnaean hierarchy is not an adequate representation of such a vertical classification, since the species category

classifications of fossil organisms, if it is understood that the taxa which should be monophyletic belong to the systems of particular time periods. The extent to which the same name should be applied to a series of taxa through time thus becomes a secondary question which can be decided upon other criteria, without violating the criterion that taxa be monophyletic, and Simpson's (1961) proposal to justify horizontal classification by redefining monophyly becomes unnecessary.

Crowson (1970: 251) has made the first specific proposals for dividing the geological time scale for the purposes of phylogenetic classification. His proposals clearly need to be supplemented by an examination of possible alternative ways in which the nomenclature applied to fossil organisms might be amended in order to implement them. There is an obvious gap here in the theory of phylogenetic systematics which is in need of detailed exploration.

An alternative approach to the classification of fossils is to relate them to the system of recent organisms, as has been done in Hennig's (1969c) book on the phylogeny of insects. A consequence of this procedure is that the rank of the lowest groups to which fossils can be referred is proportional to the age of the latter. Thus, if the boundary between the Lower and Upper Cretaceous is used to define the family category, earlier fossils cannot be referred to any family in the system of Recent organisms, but only to higher groups. In the present work I am not concerned directly with the classification of fossils, and discuss them solely in relation to the classification of recent organisms.

Some authors have interpreted Hennig's principles as entailing (for instance) the classification of every new Precambrian species in a new phylum, which they consider to be a *reductio ad absurdum* of the principles. This is a misunderstanding. New Precambrian species can be arranged by the use

of lower categories in a hierarchical system of Precambrian organisms. If discussed in relation to the system of Recent organisms, Precambrian species not referable to any Recent phylum can only be referred to a group of higher rank (e.g. the Metazoa). The description of new "phyla" is not entailed.

Since the species in a phylogenetic system are in principle species at a particular point of time, the question of how the species concept should be extended in the time dimension is only of secondary importance for the theoretical foundations of the system. Species are discrete at any given point of time, but form part of a continuum when extended in the time dimension. The breakdown of this continuum into discrete sections for the purpose of classification is necessarily an arbitrary procedure. Hennig argues that the best method is to delimit species in time by two successive processes of speciation, because it is these processes of speciation which determine the phylogenetic relationships between living species. This proposal is logically consistent. But serious doubts have been raised about the practicability of delimiting fossil species in this way, because of difficulty in establishing with sufficient precision when speciation has occurred. Even when continuous fossil sequences are available (as in some marine deposits), the geographical extent of the relevant record is usually limited, and therefore the times at which geographical speciation may have occurred can rarely be postulated with much confidence. The known fossil record of insects contains enormous temporal, as well as geographical, gaps and the fossil species as we know them are delimited by these gaps, not by theoretical principles which we may wish to apply. The possibility of devising a theoretically consistent approach to the delimitation of fossil species thus has little immediate priority for entomologists, and is mainly of concern to workers on marine fossils.

2.2. The comparative merits of phylogenetic systematics and other approaches to the classification of organisms

So far I have attempted to justify in terms of theoretical consistency the view that a phylogenetic (cladistic) classification of organisms can be presented in the form of the traditional Linnaean hierarchy. Of course the conclusion that the phylogenetic system can be so presented does not necessarily show that it ought to be. This also depends on the further question, whether the phylogenetic system is to be preferred over any other types of system which can be presented in this form. For purposes of the present argument the alternative approaches to biological classification which are currently advocated for representation by the Linnaean hierarchy are broadly grouped into two main types: phenetic classification ("typological classification" in the sense of Hennig 1966a; including "numerical taxonomy" in the sense of Sokal and Sneath 1963), and the kind of approach which Mayr (1969) calls "evolutionary taxonomy", based on combining phylogenetic and phenetic principles of classification (called "syncretistic system" by Hennig 1966a). I refer to the latter as combined classification in this work, since the term "evolutionary taxonomy" has been applied by some authors to phylogenetic and combined systematics without distinction.

In judging the merits of classification systems I follow the view that "of the many properties that could be used to construct a classification, those causally connected to many others are the most fruitful because they group the elements of the classification into classes whose names function not only in the most inductive generalizations but in the most theoretically significant generalizations" (Hull 1969, summarizing the work of Hempel 1965). Some recent authors have claimed that information retrieval is one of the main purposes of classification systems (for instance, Mayr 1969).

But in my opinion this emphasis is misplaced. Information retrieval systems should be as simple as possible in the interests of efficiency, and it hardly seems reasonable to suggest that biologists have developed an elaborate hierarchy with fifteen to twenty categories in common use primarily to act as an information retrieval system. Linnaeus' original five categories were already more than is needed for this purpose. Certain categories in the Linnaean hierarchy, particularly the species, genus and family, clearly have an important function in existing information retrieval systems; but this does not apply to the Linnaean system as a whole. The use of some of the categories in information retrieval systems leads to a conflict of interest among users of the classification. Those who are not directly interested in comparative (systematic) research often view revisions of the system with disfavour, however good the reasons for them, because stable nomenclature facilitates rapid information retrieval. If this conflict of interests becomes more severe in the future, it may become desirable to devise an independent information retrieval system which will not be affected by revision of taxa above the species level (for instance, by allocating numbers to each species).

Phenetic classification

Many pheneticists, like phylogenetic systematists, are striving to construct a theoretically consistent system, and there is no reason why both phenetic and phylogenetic systems, if both are possible, should not coexist and be mutually illuminating. I think it unfortunate in retrospect that bad relations were engendered between the two schools by Sokal and Sneath's (1963) attack on the validity of phylogenetic systematics, on the grounds that evolutionary reasoning is inherently circular. The arguments which they put forward have since been shown to be unwarranted (Hull 1967).

It is doubtful whether such extreme views are still held by the authors, since one of them has subsequently published a method of reconstructing phylogeny (Camin and Sokal 1965). Some confusion has been engendered by Sokal and Sneath's use of the term "numerical taxonomy". Numerical approaches are possible to many different kinds of classification (including phylogenetic classification, various ecological classifications, etc.), and the description "numerical" is thus potentially ambiguous. Later authors have justifiably substituted the term "phenetic taxonomy" for Sokal and Sneath's proposed classification of organisms on the basis of similarity. The attempt to classify organisms on the basis of similarity is by no means new, having historical antecedents in the school of idealistic morphology ("typology" in the strict sense), which had roots in pre-evolutionary thought of the 19th century (see Simpson 1961). Idealistic morphologists thought of species and higher groups as static entities which corresponded to unvarying "archetypes". Some held that the latter were equivalent to Platonic forms. But the metaphysical beliefs of Plato have long since fallen from favour in this field, and I do not consider them in this work.

The numerical approach to phenetic classification outlined by Sokal and Sneath (1963) presents many theoretical difficulties. The authors aimed at quantifying overall similarity, but unfortunately did not discuss the nature of this concept in detail. The only definition given (page 50) reads: "Overall similarity (or affinity) between any two entities is a function of the similarity of the many characters in which they are being compared". Taken literally this definition implies that overall similarity is an arbitrary function, which varies according to the characters used in any comparison. But probably this was not intended, since elsewhere the authors speak of the characters used in particular analyses as representing "samples".

Presumably "overall similarity" is a function of the similarity between two entities in all possible characters, and the values obtained with any particular sample of characters should be regarded as approximations to this. At any rate the claim that phenetic classification can provide a general reference system for biology depends ultimately on whether the concept "overall similarity" corresponds to some real dimension which can be quantified either in relative or absolute terms. If "overall similarity" is a concept which does not correspond to a single natural dimension, phenetic taxonomists will always be faced with the possibility of presenting a variety of different systems, depending on which characters are chosen, how they are coded and how they are weighted. Some of these systems may be useful for some purposes, but it will be impossible to extend any one system over an extensive array of organisms because of the limitations imposed by the applicability of the chosen character set. Sokal and Sneath seem to regard overall similarity as a function of genetic similarity, but this does not alter the problem since genetic similarity is a concept of the same kind (meaning the "overall similarity" between two genomes). If overall similarity (or genetic similarity) is a real single dimension, phenetic classifications based on different classes of characters should become increasingly congruent as the number of characters used is increased. I do not think that this has ever been convincingly demonstrated, and some studies definitely suggest that it is not the case (see the discussion by Ehrlich and Ehrlich 1967). Relevant data have been presented in recent discussions of the "nonspecificity hypothesis" ("Here we assume that there are no distinct large *classes* of genes affecting exclusively one class of characters such as morphological, physiological, or ethological, or affecting special regions of the organism such as head, skeleton, leaves"; Sokal and

Sneath 1963: 85). But it seems to me that more than the relations between the genome and the phenotype is at stake. If classifications based on different classes of characters do not become more congruent as the number of characters is increased, then the fundamental assumption that the overall similarity between two organisms is a parameter which can be approximated by taking samples of characters is suspect. The status of the values for similarity (or dissimilarity) produced by phenetic analyses thus requires clarification. It is obviously important whether these values can be regarded as estimates of an underlying parameter ("overall similarity") or are merely values generated by the arbitrary coding of the particular character sets used in particular analyses. If the latter is the case (as I believe), the frequently voiced claims of "objectivity" for such values and the classifications derived from them are unfounded.

Johnson (1970) has presented an important critical review of the mathematical assumptions of numerical pheneticists. According to Johnson the claims of objectivity and precision made by this school are ill-founded, and there is no hope of extending precise quantitative mathematics to describe the biological situations encountered in taxonomy. Ghiselin (1969) dismisses the concept of overall similarity as "nonsense", because there is no finite number of characters or attributes of an organism; he maintains that statements about similarity only have meaning if all the terms of the similarity are supplied.

Apart from doubts about the objectivity of the similarity values produced by numerical phenetic studies, serious doubts can be raised about the merits of converting such values into a hierarchical system. Similarity (or dissimilarity) values constitute a matrix which can only be converted into a hierarchical system by compression, with consequent loss of information.

The steps involved in converting similarity matrices into other forms of presentation have recently been discussed by Carmichael and Sneath (1969), whose views should be authoritative in view of their experience in this field. These authors state:

"Dendrograms have the advantage that they do not produce a linear ordering of the OTU's [Operational Taxonomic Units]. However they achieve this by not specifying the relation between individual OTU's, except for the initial pairs in any stem . . . OTU's in widely separated stems may be more similar to each other than to some of the OTU's in their own stems . . . A dendrogram may be thought of as a "best-fit" model compressed into one dimension by preserving the proximities between the closest pairs in each stem and averaging the remainder in a successively more general manner. It may be a successively more distorted manner if the relations among the OTU's do not permit a linear representation, or are not strongly hierarchical. Where a linear ordering is applicable and the OTU's form strongly hierarchical subsets, a dendrogram may be the simplest satisfactory display."

Thus it seems that a dendrogram is a satisfactory representation of phenetic relations only when these relations are strongly hierarchical, for instance if they tend to correspond with the underlying phylogenetic relationships (which are necessarily hierarchical). In cases where the phenetic relations appear more reticulate and diverge strongly from phylogenetic relationships, a dendrogram is not an adequate representation. From Carmichael and Sneath's comments it appears that the only useful information about the phenetic relations between species which is always retained in a dendrogram is that the pairs of species linked at the final dichotomies of each stem are most closely related to each other. No unambiguous information is retained about the relations of any species linked to a stem before the final dichotomy. Because of this loss of information, few inferences can be made about the distribution of similarity values in the original matrix. Of course the same limitations apply to the representation of phenetic relations in a Linnaean hierarchy, whose properties are similar

to those of a dendrogram.

If a hierarchical system so inadequately represents phenetic relations, it is reasonable to question the assumption of many phenetic taxonomists that such a system of classification should be the end-product of their work. This assumption seems to be linked with the belief that biologists are so used to hierarchical systems that they will reject any other type of classification. In my opinion this viewpoint obstructs real progress in the field of phenetic classification, since any objectivity or usefulness that may be credited to similarity values has been largely lost by the time these have been converted into a hierarchical system. The Linnaean hierarchy conveys information about phenetic relations inefficiently, but can be an adequate representation of phylogenetic relationships (see previous discussion). For this reason I think that progress in all fields of systematics would be better served if numerical pheneticists did not try to represent their classifications in the traditional Linnaean hierarchy, but concentrated on developing whatever forms of classification are best suited for representing phenetic relations. Mutual illumination between the different kinds of classification might then tend to replace the polemics which have been so prominent in recent literature.

From the considerations presented above I conclude that many of the claims made by Sokal and Sneath (1963) were overoptimistic, and that a widely useful hierarchical system cannot be generated from a static (phenetic) coding of character states which does not take account of their evolution.

Phenetic classifications can still be based on non-numerical methods, and indeed such attempts are faced with fewer methodological difficulties than those which face numerical phenetics. Often such classifications result from studies of a particular complex of characters, such as Rohdendorf's

(1964) classification of the Diptera, which was based on his analysis of the functional types of dipterous wings. In so far as such classifications present the results of morphological research, they may be useful and influential. The argument against preferring any such "morphological" classification to a purely phylogenetic system is based mainly on what Crowson (1970) calls the non-congruence principle. According to this principle the distribution of character states is rarely coincident, unless they are functionally correlated. This is why authors who have made investigations of a particular functional-morphological complex have so often been led to propose classifications which conflict with those based on earlier investigations of other characters. The well-known incongruences between imaginal and larval classification in some groups of insects illustrate this point. And in the order Diptera an excellent example of the classificatory problems posed by non-congruence is the long-standing dispute on whether the primary division of the order should be between Nematocera and Brachycera, or between Orthorrhapha and Cyclorrhapha. If the distribution of character states within a group is considered from a static (phenetic) standpoint, non-coincidence of the points where major structural differences occur cannot be resolved in the construction of a classification except by arbitrary choice. Different workers may well wish to make divisions at different points, in accordance with their varying interests. In fact there may be a large number of reasonably useful morphological-phenetic classifications which could be presented for groups in which the pattern of character state correlations is complex. For this reason I think that static presentations of the distribution of functional-morphological types should be regarded as special-purpose systems, and that the synthesis of all comparative data available on organisms for presentation in the Linnaean hierarchy should be

undertaken through application of the principles of phylogenetic systematics. In phylogenetic systematics incongruences in the distribution of character states are not treated arbitrarily, because the sequence in which divisions should be made is determined by reference to the time dimension.

Combined classification

For purposes of this discussion I take the work of Mayr (1969) as representative of the views of advocates of combined ("evolutionary") classification. The controversy between this school and phylogenetic systematists should not be allowed to obscure substantial agreement on many questions (such as the definition of species). The main area of disagreement is that Mayr rejects Hennig's proposals for achieving an unequivocal correspondence between phylogeny and classification above the species level. Mayr criticizes these proposals mainly on the grounds that no account is taken of different rates of evolutionary change in different lineages.

However the implication of such criticism that phylogenetic classifications ought to be corrected in some way to reflect varying rates of evolution raises serious logical difficulties. Rates of evolution can be estimated on a reasonably objective basis only for particular character sequences (particularly metric characters), but it is doubtful whether the application of such a concept can be extended to whole organisms (in other words, to the totality of their infinite attributes). Any attempt to estimate rates of evolution in the latter sense in a non-arbitrary manner must lead into the same logical morass which confronts attempts at estimating "overall" similarity, gaps between whole organisms, etc. (see Johnson 1970). Even if this difficulty could be overcome, there would remain the further difficulty that the Linnaean hierarchy is only an adequate representation of one dimension, and that consequently ambiguity must result from attempting

to use it to represent more than this (see Hennig 1966a: 77).

The differences between Hennig's and Mayr's views may be further illustrated by comparing how they define the categories. They are in full agreement in demanding a definition of species which reflects their role as the units of evolution. ("Species are groups of interbreeding natural populations that are reproductively isolated from other such groups"; Mayr 1969). But their views on the definition of categories above the species level are strongly divergent. Mayr (1969: 92) defines the genus as "a taxonomic category . . . which is separated from other taxa of the same rank (other genera) by a decided gap". He then defines the family similarly. These definitions are logically unsatisfactory because they include the term to be defined (*definiendum*). Hennig's proposal to define categories above the species level in terms of the age of origin of the stem species of the member taxa is not open to this objection, and to the best of my knowledge stands as the only proposal for an empirical definition of such categories which is not open to logical objections. Of course there are practical difficulties in many cases in applying Hennig's proposals at this time due to inadequate knowledge, but this does not affect their validity in the long term.

In my opinion Hennig's thesis that the Linnaean hierarchy should be used to represent only phylogenetic relationships (in the sense of recency of common ancestry) is not weakened by criticisms that it is too restrictive, so long as no satisfactory alternative is demonstrated. I do not find in Mayr's work any sufficient discussion of the logical difficulties inherent in his concept of a classification which reflects both cladistic relationships and evolutionary divergence at the same time. The principles of "evolutionary classification" as currently formulated do not provide

sufficient guidance on how classifications above the species level should be revised as new information is obtained. Various different criteria are suggested for the ranking of taxa, with the question of which should be given weight in particular cases left to the arbitration of the classifier. As a result no satisfactory empirical definition of categories above the species level is possible.

Acceptance of Hennig's view that the Linnaean hierarchy should represent only phylogenetic relationships (recency of common ancestry) does not necessarily imply a denial of the importance or interest of rates of evolution. Estimates of rates of evolution can be presented as a separate classification, as for instance in the diagrammatic presentations discussed by Wagner (1969). However, there can be no one correct estimate of the rate of evolution of whole organisms because of the multidimensional nature of the data. Whether there is any other dimension except time to which rates of evolution can be referred is not clear. I do not exclude the possibility that they can also be referred to some determining factor at the genetic level, in which case an alternative kind of evolutionary classification to phylogenetic classification in Hennig's sense could be devised. But so far this possibility has not been demonstrated.

Phylogenetic classification

The claim that the phylogenetic system is a useful reference system for biology rests on the fact that "there is one dimension to which all other dimensions are referred, and that is the time dimension" (Brundin 1966). Since there is only one phylogeny of any group of organisms, phylogenetic systematists are not beset with theoretical difficulties in reconciling the evidence of different classes of characters. All available comparative information can and should be considered. Because the phylogenetic system

is congruent with a real common dimension, its conclusions are not logically dependent on the use of a particular suite of characters in analyses, and the system can be extended to include all the organisms of a particular time period. Herein lies one of the reasons for claiming superiority for the phylogenetic system over phenetic systems. The latter are inevitably restricted in their extent because of their dependence on particular character suites.

The usefulness of a consistent phylogenetic system in which phylogenetic relations (recency of common ancestry) are expressed without ambiguity is clear enough for those branches of biology which make historical comparisons between organisms. Historical biogeography is an obvious example. It is perhaps not so obvious that the use of a logically consistent phylogenetic system also has significant advantages for branches of biology which compare only Recent organisms. Comparative morphologists employ a concept of homology which is usually defined in terms of common origin in time (evolutionary homology). Statements about homology in this sense are best expressed through a classification of monophyletic groups, since only such groups have a unique common origin in time. In fact comparative morphology cannot be divorced from phylogenetics, if an evolutionary definition of homology is accepted. Phylogenetic classifications are therefore very relevant to studies of comparative morphology, as well as morphological-phenetic classifications of particular character complexes. A more general case for the relevance of phylogenetic classification to comparisons between organisms, apart from the special question of the use of an evolutionary criterion of homology, can be made in terms of the predictive value of such classifications. This can be a question of practical importance in relation to attributes which can only be demonstrated after

laborious studies. For instance, if an unusual physiological process has been demonstrated to occur in a small number of rather remotely related species, how widely is this process likely to occur? Predictive answers to questions of this kind are best made by reference to the monophyletic taxa of the phylogenetic system. Such predictions are less reliably made from morphological-phenetic classifications, unless there is a close functional correlation between the character suite used to construct the classification and the attribute whose distribution is predicted. Therefore, I think that over a wide field of biology the phylogenetic classification is the classification which best meets Hempel's criterion of functioning in the most inductive generalizations. Further arguments for the special position of the phylogenetic system in biological research have been given by Hennig (1950, 1966a).

It is appropriate here to refer to the distinction between general-purpose ("natural") and special-purpose ("artificial") classifications made by Gilmour and his followers (the "philosophical school" of taxonomy). I accept the general view that this distinction is useful, although there are logical difficulties involved in attempting to apply it in a precise way (see Johnson 1970). Gilmour and Walters (1964) define these terms as follows:

"General-purpose classifications consist of classes containing objects with a large number of attributes in common, thus making them useful for a wide range of purposes; special-purpose classifications consist of classes containing objects with only a few attributes in common, and hence serve a more limited range of purposes."

If we attempt to read some operational significance into these definitions, they seem to suggest that we can form a judgement on whether a classification is general-purpose or special-purpose by enumerating attributes in

common. However, the term "attributes" is so indefinite that enumeration of attributes is only possible if the range and kind of attributes to be considered is specified; in which case the validity of any conclusions for demonstrating *general* purposiveness would be in doubt. Recourse to an all-attributes concept would lead us into a "hopeless morass" (Johnson 1970). For this reason Gilmour's distinction can only be applied in a vague qualitative way. We can try to consider what *kinds* of common attributes are possessed by the classes of objects in particular classifications, or in what fields of enquiry these classes are useful for conceptualization and communication. My attempt in the preceding paragraphs to demonstrate that the phylogenetic system is useful in many different branches of biology can thus be considered an attempt to demonstrate that the phylogenetic system is a "general-purpose" biological classification. But it is not necessarily the *only* general-purpose classification of organisms. Probably some form of ecological classification of organisms can also be regarded as a general-purpose system. In the latter case the "powerful factor" (in the sense of Gilmour's and Walter's seventh principle) which makes a general-purpose system possible is not phylogeny but the flow of energy through the biosphere.

The definition of general-purpose classifications given by Gilmour and Walters seems to me only partial. They do not demand that the classes included in any particular classification shall be homogenous, nor do they attempt to clarify the significance of the formal relations between classes in classifications. A sufficient definition of general-purpose classifications should surely also refer to these aspects. The point may be illustrated with the words of Lewis Carroll's Walrus. '

"The time has come," the Walrus said,
 "To talk of many things:

Of shoes—and ships—and sealing wax—
Of cabbages—and kings. . ."

(Lewis Carroll, *Through the Looking-Glass*)

The five classes of objects in the last two lines doubtless all function in general-purpose classifications, but should not be included in the *same* classification. The definition of general-purpose classifications given by Gilmour and Walters says nothing to discredit the Walrus' ability as a taxonomist. I conclude that the definition requires elaboration. Gilmour and Walters were unable to suggest any clearly defined procedure for classifying through the Linnaean hierarchy. Their only comment on the use of categories is that comparatively few changes should be made in the ranking of taxa in the interests of stability of nomenclature. This is hardly consistent with their general thesis, since the categories are classes and ought therefore to indicate common attributes of the objects referred to them in a general-purpose classification.

The conclusion which I draw from the considerations presented above is that the phylogenetic system is a general-purpose classification widely useful in many branches of biology, and that it is the most suitable classification for representation through the Linnaean hierarchy. But this does not imply that it is the only useful kind of classification, nor the only possible general-purpose classification. Other kinds of classification are useful in most, if not all, fields of biology. If misunderstanding and conceptual confusion are to be avoided, other kinds of systems should be presented independently of the phylogenetic system. There are no grounds for supposing it possible to produce a single optimal classification which is useful for all possible purposes.

Revision of the Linnaean hierarchy to represent phylogenetic relations is not inconsistent with the recent history of systematics. In practice,

most recent revisionary work has tended to change classifications so that the proportion of monophyletic groups in the system is increased, even when the authors have not adopted any consistent theoretical standpoint. For instance, if the history of changes in the ordinal classification of insects is considered, the trend to break down polyphyletic or paraphyletic groups (such as the Linnaean "Neuroptera") is readily apparent. Nearly all the orders currently accepted in the classification of Recent insects are believed to represent monophyletic groups, with possible exceptions only in areas where the phylogenetic relationships require clarification (e.g. Mecoptera).

2.3. Procedures of phylogenetic analysis

Hennig (1950, 1966a) discusses in detail the analytical procedures involved in constructing phylogenetic classifications. He distinguishes three methods, the comparative holomorphological method, the paleontological method and the chorological method. In this work I employ the comparative holomorphological method to produce a phylogenetic classification of Recent species. My remarks are therefore concerned mainly with the use of this method.

Theoretical considerations

The starting point of Hennig's treatment of the comparative holomorphological method is the observation that phylogenetic relationship is not proportional to similarity, because there are demonstrated differences in the rates of character change in different phyletic lineages. Community of descent can be inferred from common possession of the apomorphous conditions of any character sequence (synapomorphy), but not from common possession of plesiomorphous conditions (symplesiomorphy).

Hennig's terms "plesiomorphous" and "apomorphous" are equivalent to the more familiar terms "ancestral" and "derived". I use the former terms in this work, since they have no conflicting meanings arising from usage outside biological systematics, and since they can be readily compounded to form such words as "synapomorphous", "autapomorphous" etc. These concepts can only be rendered clumsily using the ancestral/derivative terminology: for instance, the autapomorphous characters of a group would have to be referred to as "those derivative characters of a group, which are not shown by species outside the group". Hennig's terminology was first proposed in the German language (as "plesiomorpher", "apomorpher" etc.) and has been variously rendered into English. I here follow the English forms given in Hennig's (1966a) book. The terms "plesiomorphous" and "apomorphous" refer properly only to morphological characters, but similar terms are available for characters of other kinds, such as "plesiooecous" and "apooecous" (for ecological characters) and "plesiochorous" and "apochorous" for distributional characters. Tuomikoski (1967) has appropriately suggested that the more general terms "plesiotypic" and "apotypic" may be used to embrace all kinds of characters.

The observation that taxa should only be characterized by apomorphous (derivative) conditions in their groundplan is, of course, by no means new, and to many people seems self-evident. But Hennig was justified in laying great emphasis on this principle, since many authors have not followed it. After exploring the implications of this principle, Hennig proposes the "argumentation scheme of phylogenetic systematics" (fig. 3) as a model for the performance and presentation of phylogenetic analyses.

In the argumentation scheme the grounds for a phylogenetic hypothesis are illustrated by superimposing an interpretation of character states on

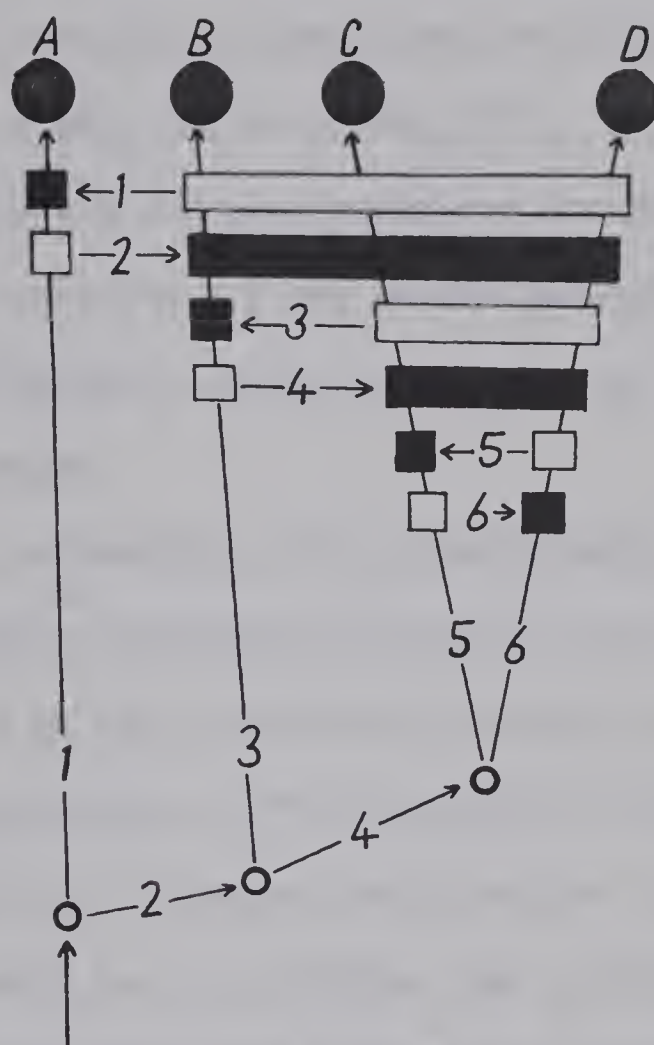


Fig. 3. The argumentation scheme of phylogenetic systematics (after Hennig 1966a). All groups regarded as monophyletic are distinguished by the possession of derived (apomorphous) stages of expression (black) of at least one pair of characters (synapomorphy of species of monophyletic groups).

a dendrogram. It is conventional to use black rectangles for apomorphous states, and white rectangles for plesiomorphous states. If the number of characters considered is too large for convenient presentation in this form, the postulated branching sequence may be indicated by brackets above a table of character states (as in my fig. 17).

The terms apomorphous and plesiomorphous are relative. The apomorphous conditions which characterize a group become plesiomorphous ("outside primitives" in Throckmorton's terminology) from the standpoint of analysis of its subordinate groups.

In phylogenetic systematics the characterization of groups is presented in terms of their apomorphous groundplan conditions. The groundplan of a group is defined as the condition of the last common ancestral species at the age of differentiation. The groundplan is thus a historical reconstruction, not some kind of average condition for a group. An abstraction of the latter kind would be an archetype, not a groundplan. Groundplan characterization is not always the same as the diagnostic characterization presented in keys to identification, because some or even most members of a group may show conditions which represent further modifications of the groundplan condition. In considering whether or not a species belongs to a particular group, the question which should be asked is whether the conditions shown by this species are more probably derived from the groundplan conditions of this group, rather than from the groundplan conditions of any other group.

Throckmorton (1962) discusses an alternative argumentation model, based on the principle that "possession by two species of a particular characteristic will indicate only that they are derived from some common heterozygous population". He argues that if the apomorphous condition was present as

part of a polymorphism in the common ancestral species, some descendant species may show the apomorphous condition and others the plesiomorphous condition. In my opinion the use of this "balance hypothesis" model is only warranted when the character states in question are known to form part of a balanced polymorphism in some existing species, and I suspect that Throckmorton may have overextended the use of his model to cases where homoiology or parallelism would be a more probable hypothesis. At any rate one must be guided in phylogenetics, as in other branches of science, by the principle of parsimony (Occam's razor). In cases where Hennig's model (called the "classic" model by Throckmorton) provides a consistent explanation of the observed distribution of character states, I think this may be accepted as the most parsimonious explanation. In studies of the relationships between groups of high rank, we are mainly concerned with the distribution of rather strongly differentiated character states to which the balance hypothesis can hardly apply. The argumentation in this work is consequently presented within the framework of Hennig's argumentation scheme.

Hennig's scheme has been criticized by several authors (including Darlington 1970) on the grounds that it involves assuming that speciation is usually dichotomous. These criticisms raise the complex question of the nature of speciation, which I do not consider in this review. However differences of opinion on this question need not give rise to methodological disputes, if *a priori* assumptions about the extent to which evolution is dichotomous are excluded from phylogenetic analyses. I do not think that the application of Hennig's methods depends on making *a priori* assumptions of this kind, and his argumentation scheme can be readily extended to cases of non-dichotomous speciation. If the pattern of character states expected

to result from a dichotomy is found (alternance of apomorphous and plesiomorphous states), then a dichotomy should be postulated as the most parsimonious interpretation. But if such a pattern is not apparent, a dichotomous classification should not be presented.

Darlington (1970) has expressed several further criticisms of the procedures outlined by Hennig (1966a) on the grounds that they involve unacceptable simplifications of the processes of speciation and evolution. Unfortunately, some of Darlington's criticisms seem directed at distorted interpretations of Hennig's thought. For instance, I do not follow his argument that Hennig assumes rates of evolution and divergence in related lines to be uniform, since this is contrary to Hennig's stated opinions. Nor can I accept the argument that relative primitiveness of species or groups (not just of character states) is important to the theory of phylogenetic systematics (cladism). While the description of species or groups as relatively plesiomorphous (primitive) or apomorphous (derivative) seems meaningful in extreme cases, such statements should be avoided or at least qualified as a general rule; for non-congruent changes in different character sequences often make the extension of the concepts of plesiomorphy and apomorphy from particular character sequences to whole organisms problematical. Darlington's criticisms suggest a need for comment on the nature of the simplifications inherent in Hennig's argumentation scheme and other dendrogrammatic presentations of phylogeny and character change. That these presentations are very simplified is not disputed, for Hennig (1966a: 88) introduces the diagram of speciation (reproduced by Darlington as his figure 1) with the words "in this simplest possibility". Simple conceptual models are plainly useful in many fields of science, and there is no reason why we systematists should be denied the use of such models.

The customary presentation of phylogeny as a dendrogram is already a highly simplified conceptual model, and Hennig's argumentation scheme differs primarily by the addition of a representation of character states. This addition improves the model, because an unadorned dendrogram is open to the misunderstanding that the differences between species can be reduced to a single dimension. If we consider the argumentation scheme (fig. 3), the simplifications inherent in it include: (1) representation of species lineages by straight lines; (2) representation of speciation by a branching point; (3) representation of character states as uniform within species or groups of species; (4) representation of the complexly interrelated differences between organisms by separate series of character states. Clearly there are purposes for which the argumentation scheme or other form of simple dendrogram is not an adequate analytical model because of these inherent simplifications (for instance, detailed analysis of a speciation process). But this restriction applies to all conceptual models, without exception (including those presented as mathematical formulae). The usefulness of models should be judged primarily in relation to the purposes for which they are proposed. It is not warranted to discuss a model in relation to some purpose for which it was not primarily intended, demonstrate its inadequacy for this purpose and then pronounce it useless for any purpose. If true, this kind of argument would invalidate much of what we now accept as theoretical biology. Darlington's conclusion that many of Hennig's models ("concepts") are of no practical use seems to rest, at least in part, on unwarranted reasoning of this kind. The diagrams from Hennig's (1966a) book which Darlington reproduces and criticizes were introduced by Hennig in a discussion on "the rules for evaluating morphological characters as indicators of degree of phylogenetic relationship"

in a section on the delimitation and ranking of groups above the species level. The argumentation scheme and other simple dendrograms used in that section are in my opinion adequate for character evaluation and analysis of the relationships between species and groups of species, so long as the variation within species (or groups of species) which is concealed by the definition of character states is slight in relation to the differences between the character states. Although I disagree with much of what Darlington says, I see value in his paper as providing a warning against our losing sight of the simplifications inherent in the analytical methods proposed by Hennig. The only proof against the misuse of conceptual models in contexts in which they may be misleading is an awareness of their limitations.

Evaluation of characters

The construction of phylogenetic classifications involves judgements about the sequence of character changes, and the distinction of probable synapomorphies from other types of resemblance (homoplasy). Such judgements require a detailed knowledge of the organisms concerned, as well as an understanding of the principles of phylogenetic analysis. The criteria which can be employed in forming such judgements have been well discussed in general terms by Hennig (1950: 172, and 1966a: 93), and I do not give an extensive review here.

Homoplasy is defined as "resemblance not due to inheritance from a common ancestry" (Simpson 1961), and is equivalent to the wide sense in which the term "convergence" has been used by some authors. In this work I use three terms to denote types of homoplastic resemblance: convergence, parallelism and homoiology. In practice not all cases of homoplasy can be classified unequivocally with this terminology, but a rough distinction can

be made. The term convergence in the restricted sense here followed is applied to homoplastic character states which are the result of different transformation sequences. The acquisition of similar character states independently by different species, but without different transformation sequences, is called parallelism. When conditions are thought to have the same genetic base and to reflect close kinship among their bearers, although the phenotypic change occurred independently, they may be called "homoiologous". Homoiology thus occupies an intermediate position between parallelism and true homology.

One of the main problems confronting attempts at phylogenetic analysis is the need to distinguish conditions acquired through parallelism or homoiology from truly synapomorphous conditions. Convergence in the restricted sense rarely results in conditions so similar that they are likely to be mistaken for synapomorphous conditions, except in some reduction sequences (such as in the wing venation of Diptera). The detection of convergence in such cases clearly depends on reconstruction of the transformation sequences. In general the most useful criteria which can be employed in evaluating character states are the following: (1) the criterion of genetic complexity of character change ("Kriterium der Kompliziertheit der Merkmale", Hennig 1950), and (2) the criterion of compatibility with the distribution of other apomorphous character states. Doubts have been raised about the validity of Darwin's distinction between "adaptive" and "non-adaptive" characters for purposes of evolutionary evaluation, and I therefore do not employ such a criterion. Both the criteria which I employ lead to probability judgements. The justification for employing the "criterion of complexity" is that the amount or complexity of genetic change required to bring about particular changes in phenotypic character states is not constant.

The change from a plesiomorphous to an apomorphous condition may involve anything from a change at a single genetic locus to an extensive reorganization of the genome. This is why the "non-weighting" procedure recommended by some numerical taxonomists is invalid for phylogenetic analysis. Clearly the odds against the same character change having occurred through homoiology or parallelism must increase in relation to the complexity of the required genetic changes. In cases where considerable genetic complexity is believed to be involved, such as when new and complex structures have been acquired, the possibility that the whole of the genetic changes involved may be ascribed to homoiology or parallelism becomes so negligible that it may be discounted. The same thought probably underlies Remane's (1952) conclusions on the applicability of the law of irreversibility ("Dollo's law"). He states that the law should not be applied to proportional relationships, quantitative differences, etc., but can be applied without restriction to complex organs, because no case of the reappearance of complex organs after loss has ever been demonstrated.

The validity of the criterion of genetic complexity would be doubtful only if evolution were a predominantly convergent or equifinal, rather than divergent, process. In that case phylogeny would be relegated to a subordinate process in evolution, and a classification of monophyletic groups would be of very limited value. I follow the orthodox view that evolution has occurred within species and populations, and that when groups of species show major structural modifications in common, they are descended from a common ancestral species. This view has sound empirical foundation in the obvious divergence in many characters often shown by vicariant species or by separated populations of the same species.

The criterion of genetic complexity can at present only be applied in

a crude way, because the genetic basis of most character changes is not known directly. Nevertheless many inferences about the relative genetic complexity of character changes can be made from indirect evidence. For instance, it is reasonable to suppose that character changes which can be shown by viable mutants within a species may be of relatively low complexity from a macroevolutionary point of view. For this reason I see little difficulty in inferring that parallel changes have occurred in the numbers of spermathecae and of fronto-orbital bristles, when the distribution of apomorphous states of these characters conflicts with the distribution of other character states which are believed to have resulted from more complex changes. It also appears valid to assume that structures may be readily lost through convergence or parallelism; for any complex organ or system whose efficiency ceases to be maintained by selective pressure is likely to degenerate due to the pleiotropic effects of genetic changes (as in the many unrelated cavernicolous animals which have become blind).

The criterion of genetic complexity should not be applied in isolation, but only in conjunction with the criterion of compatibility. This criterion was treated by Hennig (1966a: 120) as the "method of checking, correcting and rechecking". I have applied this criterion by setting up hypotheses about the limits of monophyletic groups based on the distribution of particular apomorphous character states, and then by checking these hypotheses for compatibility with the distribution of as many other apomorphous character states as possible. There is no restriction on the kinds of characters which can and should be compared, since all the characters of organisms have evolved in time. Therefore, the true transformation sequence of all characters must be compatible. Apparent incompatibilities revealed by the analysis may often be resolved by consideration of the numbers of

characters which support alternative hypotheses and their probable complexity. Many hypotheses may be rejected, or considered too doubtful to be expressed in the formal classification. In evaluating hypotheses one should always bear in mind Hennig's "auxiliary principle", that the presence of apomorphous conditions in different species is always reason for suspecting kinship, and that convergence or parallelism should not be assumed *a priori*. This "auxiliary principle" is an application of the principle of parsimony (Occam's razor). It is warranted to postulate from character changes of low complexity that certain species constitute a monophyletic group, if this hypothesis is compatible with the evidence of other characters. Common apomorphous conditions should not be ascribed to homoiology or parallelism unless the hypothesis that they are synapomorphous is incompatible with other evidence.

Tiegs and Manton (1958) claim that "where specialization confers so many advantages the condition for almost unlimited convergence arises". They proceed from this premise to postulate a diphyletic origin of the Arthropoda. I do not think that the evidence which they present justifies their rejection of the view that the most probable phylogenetic hypotheses are those with minimal postulated homoplasy. The fossil record does not demonstrate that different transformation sequences have led to "arthropodization" in the Myriapoda-Insecta on one hand and the Crustacea-Chelicerata on the other.

Cain and Harrison (1960) have presented an important discussion on the detection of homoplasy ("convergence" in their sense). They argue that homoplasy between closely related groups is likely to be common, particularly in respect of "necessary functional correlates". Clearly there is truth in this argument at the level of parallel changes in proportions, quantita-

tive differences, etc.; some groups of species do in fact display a reticulate pattern of resemblances, which suggests that many parallel or homoiologous changes have occurred. While accepting the opinion of Cain and Harrison that some cases of homoplasy are likely to remain undetected, I do not think this in conflict with the principle that the most probable approximation to a classification of monophyletic groups is that with minimal postulated homoplasy.

Numerical methods

Recently several different methods of numerical analysis have been suggested for phylogenetic studies. Edwards and Cavalli-Sforza (1964) proposed a Prim Network forming procedure intended primarily for analysis of racial evolution. I doubt whether this method is useful for studies of macroevolution, since it incorporates some assumptions which seem unrealistic in this context (such as random drift of characters). Camin and Sokal (1965) presented a method for reconstructing probable phylogenetic relationships by comparing the evolutionary patterns suggested by particular character sequences against one another. Such checking for compatibility of hypotheses suggested by particular character sequences is in my opinion a necessary part of the method of phylogenetic systematics. But I do not think that Camin and Sokal have adequately treated this question. The pattern tables for the character sequences given in their paper include groupings formed on the basis of symplesiomorphy, and the compatibility matrices consequently exaggerate the apparent conflicts between the evidence of the different characters. I also do not follow the logic behind their "monothetic method", which seems to involve grouping species on the basis of minimal number of retained plesiomorphous conditions (zeros in the matrix), irrespective of whether they show the same or different apomorphous conditions.

Throckmorton (1968) has suggested a procedure based on complete linkage analysis, but Farris, Kluge and Eckardt (1970) have questioned the value of this method on the grounds that some useful information is lost. The latter paper probably provides the best introduction to recent work in this field.

The use of mathematical analysis may well prove of value in some circumstances, but I wish to interject a word of caution. The methods of numerical phyletics, like those of numerical phenetics, presuppose the metaphysics of logical atomism. According to logical atomists the world of experience can be analysed into basic atomic facts or sentences which are not logically subdivisible. The atomic facts relevant to the classification of organisms are now called "unit characters", following Sokal and Sneath (1963). The unit characters are assumed to be all homogenous, and in order to reduce the most highly heterogenous data to a common base for mathematical handling, all that is necessary is to express the data in terms of unit characters. The frequent claim that "non-weighting" of characters (giving a set of characters equal weight) is "objective" clearly reveals the nature of these hidden assumptions. Unfortunately, there are no empirical grounds for the belief in the existence of atomic facts or unit characters in the sense of homogenous independent units like physical atoms. In the 1920's and 1930's some philosophers, inspired by the early works of Ludwig Wittgenstein, tried to reconstruct language from atomic facts or sentences. But these efforts are now generally considered to have been unsuccessful. In view of the demise of logical atomist ideas in the field of philosophy, the unquestioning assumption of such metaphysics in a very simple form by some mathematically oriented biologists seems to me naive. If the characters of organisms are not analysable into homogenous

atomic ("not logically subdivisible") units, then the belief that there is anything "objective" in the procedure of treating heterogenous characters as if they had a common metric base is without foundation, and it should be recognized that arbitrary decisions are taken in the choice, definition and weighting of characters. A further consequence is that the problem of evaluating characters cannot be willed away by assuming that all "unit characters" are equal. Probably the nearest approach to a unit basis for character change lies at the genetic level, but even here there are problems of interpretation (in particular, the equifinal nature of many biological processes at the molecular level).

If my denial of logical atomism is correct, then numerical phyletics cannot supplant the traditional approach to phylogenetic analysis elaborated in Hennig's works. At most it can provide supplementary methods, to be used with due caution in view of the arbitrary steps involved. I do not employ numerical methods in this work.

Certainty and phylogeny

The end results of phylogenetic analyses represent best estimates, approximations to the underlying phylogenetic relationships which can never be known with absolute certainty. Phylogenetic classifications thus should not be regarded as static, but must be periodically revised as our knowledge of phylogenetic relationships increases. The argument that phylogenetic systematics is non-operational because phylogeny cannot be known with certainty could be applied to the whole of natural science (see Hull 1967). Our observations of the real world and the inferences which we make from these observations are never invested with absolute certainty, and it can only be assumed that authors who demand absolute certainty misunderstand the dependence of all physical and biological sciences on inductive hypotheses.

3. The structure of the male postabdomen

3.1. Preliminary treatment and explanation of terminology

Segmentation

The basic segmentation of the abdomen in Cyclorrhapha has been well discussed by Crampton (1942), van Emden and Hennig (1956), Steyskal (1957a) and Hennig (1958). If the andrium represents the 9th segment (as now seems almost universally accepted), the numbering of the preceding segments can be established from considerations of comparative morphology. The Cyclorrhapha contain some member groups in which all eight preceding segments are clearly defined and bear discrete sclerites. The correct numbering for groups in which sclerites have been fused or lost can be established by analysis of the sequence of morphological changes which have occurred and by ontogenetic evidence, when this is available. The interpretation of the various conditions found in particular groups is discussed below in my treatment of the groups concerned. One remaining source of dispute affecting the interpretation of the postabdominal structure of all Cyclorrhapha is whether or to what extent the 8th segment is rotated. This question is discussed in detail below in section 3.2, where I present what seems to me conclusive evidence that this segment is inverted (rotated through 180°). I therefore follow Crampton in calling the dorsal sclerite of this segment the 8th sternum, and the reduced ventral sclerite the 8th tergum. Reduction of the 8th tergum to a narrow band is probably a ground-plan condition of the Cyclorrhapha (see section 4). My analysis of the relationships between the families of Schizophora has led me to explore certain sequences of modifications of the postabdominal sclerites. The starting point for these sequences seems to be the condition shown by the

Platypezidae (figs. 10 and 11), in which the 6th and 7th segments are more or less unmodified, with their respective terga and sterna developed as discrete sclerites in the normal dorsal and ventral positions, and the inverted 8th segment retains a large dorsal sternum and a band-like tergum vestige in ventral position.

The abdomen of male Cyclorrhapha is conventionally divided into the preabdomen (segments 1 to 5) and the postabdomen (segments 6 and following), following Metcalf (1921). This distinction is one of descriptive convenience, and does not reflect a fundamental morphological change between segments 5 and 6. In some groups the 6th segment is unmodified and similar to the preceding segments; in others, such as some Syrphidae, modification of the terminal segments begins with the 5th segment. Even in forms with a highly modified postabdomen, some structures (for instance the *sensilla trichodea* [fig. 89], the intersegmental musculature and the spiracles) are often readily recognizable as homonomous ("serially homologous") as far as the 7th segment. Some authors use these terms flexibly, varying the point of division according to how many segments are unmodified. However there are difficulties in applying this criterion to some families in which the 6th tergum is unmodified but the 6th sternum modified to some extent (for instance Micropezoinea and Tanypezidae). I prefer to adhere to consistent morphological definitions (following Hennig 1936a), to avoid possible misunderstanding. The term protandrium has been proposed for that part of the postabdomen which precedes the genital segment (Steyskal 1957a).

The term genital pouch may be applied, if convenient, to membranous areas of the postabdominal venter which protect the aedeagus in its rest position. However the term has no general morphological significance or implications of homology, as the extent and manner of formation of such

a pouch vary between different groups.

Genitalia (general questions)

The homologies of some parts of the external male genitalia of holometabolous insects are still the subject of dispute, mainly because of difficulties in interpreting the ontogenetic evidence. The crux of the dispute rests on whether the large lateral clasping lobes of the genital segment (usually biarticled except in Coleoptera) are homologous with the appendage articles (precoxae and styli) found on the 9th abdominal segment of Thysanura. Authors who have accepted this homology have called these lobes "gonopods", consisting of a basal "basistylus" or "coxite" and a terminal "dististylus". Van Emden and Hennig (1956) accepted this view, and stated that the work of Abul Nasr (1950) on the ontogenetic development of certain Nematocera had demonstrated the existence of true gonopods (limbs of the genital segment) in Diptera. However Abul Nasr's observations can be interpreted differently, and Snodgrass (1957: 47) explicitly rejected van Emden and Hennig's interpretation. In the same paper Snodgrass rejected some of his own earlier opinions on the homologies of the male genitalia of insects, and in particular maintained that there were no gonopods in any holometabolous insects. According to Snodgrass' interpretation the paired rudiments ("primary phallic lobes") which give rise to the supposed "gonopods" of holometabolous insects, as well as to the aedeagus and other parts of the reproductive apparatus, are homologous with the rudiments which give rise to the aedeagus alone in Thysanura. Snodgrass proposed to apply the term "parameres" to the supposed gonopods, in accordance with the original use of the term parameres by Verhoeff (1893).

The validity of Snodgrass' interpretation of the homology of the

genital rudiments of Holometabola is doubtful in view of the radical ontogenetic changes which have occurred in the evolution of this group, and Sharov (1966) has criticized his work on these grounds. Sharov states that "the external grasping appendages . . . are homologous with the precoxal plates and the styli sitting on them in Thysanura", which is simply a restatement of the gonopod theory. He does not present new evidence to support this view. Matsuda (1958) reviewed the ontogenetic evidence and raised serious objections to homologizing any part of the male genitalia of holometabolous insects with the appendage articles of Thysanura. Unless these objections can be dispelled, the gonopod theory should be regarded as not proven. Besides Snodgrass' view and the gonopod theory, a third possibility should be considered: that the parameres may be homologous with the gonapophyses of the 9th segment in Thysanura. A firm judgement between these alternatives probably cannot be made at present, because the ontogenetic changes which occurred in the evolution of the Holometabola are not well enough understood. Controversy has continued since the 1890's, and no consensus has yet emerged. In the present work I follow Snodgrass' (1957) proposal of applying the term parameres in its original sense (to the supposed "gonopods"), and calling their component articles the basimeres and telomeres (= distimeres of Crampton). This is a special terminology proposed for the genitalia of Holometabola, and has the advantage that it does not imply homologies with the structure shown by less modified insects, such as Thysanura.

E.L. Smith (1969) has proposed a revised interpretation of insect genitalia and much new terminology. Smith's interpretation and terminology are not accepted in this work, since some parts of his theory are untenable. In particular, I do not understand why he assumes that inter-

locking gonapophyses of the 8th and 9th abdominal segments (as in females of Thysanura and some pterygote orders) were an ancestral condition in male insects, since there is no known male insect (living or fossil) which shows such a condition. His view that the gonapophyses of the 9th segment have partly fused in many male Pterygota to form an intromittent tube (aedeagus) seems tenable, but he does not demonstrate why this interpretation is to be preferred to the interpretations of the origin of the pterygote intromittent organ put forward by other authors. This question depends on the interpretation of ontogenetic evidence, which Smith does not review in detail. I must also note that some of the statements which he makes about Diptera are misleading. For instance, the statement that female Diptera possess an "antovipositor", defined as an "egg-laying device where nonappendicular components dominate . . . homologous to ♂ aedeagus" is incorrect, because studies of intersexes in Diptera have not suggested that any structures of the female are homologous with the male aedeagus (see Laugé 1968). Another incorrect statement is that "potential homology has been seen" between the gonopods of both sexes in Drosophilidae; for irrespective of whether one supposes that gonopods are present in the male, there are certainly no structures which can be homologized with gonopods in female Drosophilidae. Because of such obvious deficiencies, I do not think that much weight should be given to Smith's views.

In this account of the structure of the male terminalia I include only synonyms which seem to me significant or which have been widely used. The diversity of terminology used by different authors is so great that attempts to compile complete synonymies are best left to works on individual families. This diversity has arisen not only from the dispute on the origin of the genitalia, but also because workers on cyclorrhaphous families

have found difficulty in homologizing some of the structures found in these groups with those of other Diptera. As a result various provisional terminologies have been proposed in taxonomic works.

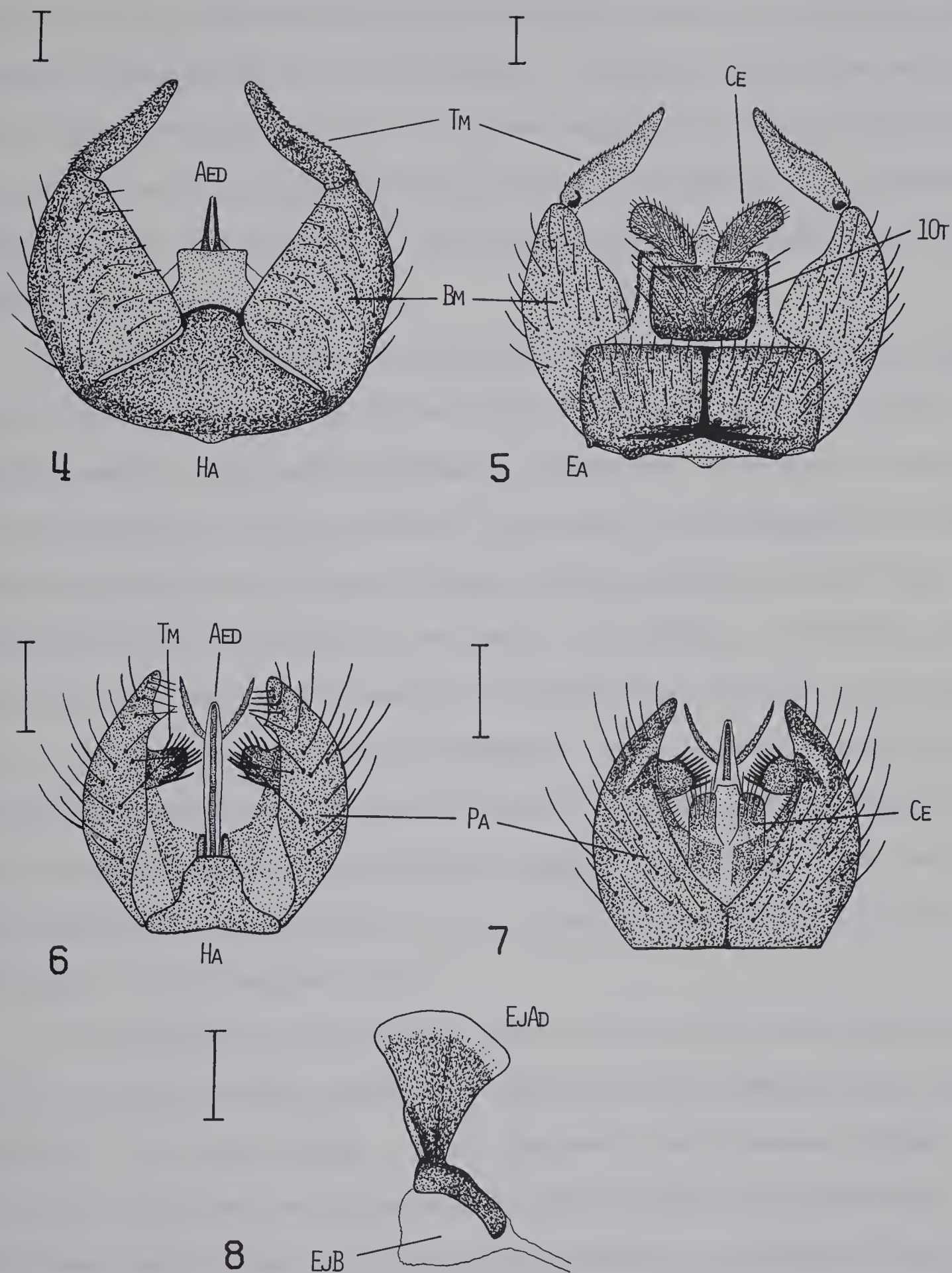
The terms hypopygium or terminalia are here used to refer to the whole of the genital (9th) segment (or andrium) and associated proctiger. I do not extend the application of these terms to preceding segments (as did Lindner 1949). Objections have been raised to the term hypopygium on the grounds that its application to structures situated above the anus (which are hence epipygial rather than hypopygial) is linguistically incorrect; but this objection loses its force, if the view advanced below that all the hypopygial structures of Cyclorrhapha are ventral in origin is accepted. The genital segment (andrium) and its associated structures are also often referred to as the external genitalia.

The external sclerites of the genital segment

The genital (9th) segment or andrium is enclosed laterally and dorsally by a large sclerite which has been assumed to be the epandrium (9th tergum) by virtually all recent authors. Hennig (1936a) maintained that this sclerite was formed by fusion of the 9th and 10th terga with the basimeres (which he called the basal articles of the gonopods). But van Emden and Hennig (1956) followed the prevailing opinion that this sclerite is the epandrium (9th tergum). There is indeed no evidence in comparative morphology or ontogeny for a fusion of the basimeres with any tergum. But there is strong evidence that the homology of this sclerite is not with the epandrium but with the basimeres. My view is that the true epandrium (9th tergum) is completely absent in the Cyclorrhapha, and that the so-called "epandrium" of this group is formed by upward growth of the basimeres (basal articles of the parameres) and their fusion along the centre of the

dorsum. Since the term epandrium should be applied only to the 9th tergum, I therefore propose for this sclerite the new term periandrium. Since my interpretation is new, further justification is needed.

The structure of the terminalia of Rhagionidae (figs. 4 and 5) is taken (following Karl 1959) as close to the plesiomorphous condition for the Brachycera (of which the Cyclorrhapha are a subordinate group). The terminalia of this family can be homologized without difficulty with the terminalia of many nematoceros families and named accordingly. The genital segment bears ventrally a triangular 9th sternum (hypandrium) and biarticled parameres, which serve as claspers during copulation. In dorsal view a well-developed epandrium (9th tergum) can be seen, and the proctiger bears a distinct tergum (tergum 10), as well as cerci. The terminalia of the Eremoneura (including the Orthogenya and Cyclorrhapha) differ from those of the Rhagionidae in several respects. The relevant information is found in Bährmann's (1960) study on the male copulatory organs in Empididae, although the conclusions which I have drawn from the data differ in some respects from those in that author's own discussion. According to Bährmann's interpretation the parameres (which he calls "Gonopoden") only occur in those genera of Empidinae and Hemerodromiinae which are characterized by a small and usually cleft epandrium. He interprets as plesiomorphous the condition shown by other groups (such as the Hybotinae, Ocydromiinae and Tachydromiinae), in which the "epandrium" covers the greatest part of the genital segment and extends laterally to overreach the ventral surface. In my opinion the character sequence is more probably the reverse. I interpret the large laterally placed basimeres of *Empis* and its relatives as indicating the plesiomorphous condition for the Eremoneura; the condition shown by the Hybotinae/Ocydromiinae/Tachydromiinae group I interpret as derived from this



Figs. 4 - 8. 4. *Rhagio* sp. (Rhagionidae), hypopygium (♂) in ventral view. 5. *Rhagio* sp. (the same individual as shown in fig. 4), hypopygium (♂) in dorsal view. 6. *Atelestus pulicarius* (Fallén) (Empididae, Atelestinae), hypopygium (♂) in ventral view. 7. *Atelestus pulicarius* (Fallén), hypopygium (♂) in dorsal view. 8. *Agromyza phragmitidis* Hendel (Agromyzidae), ejaculatory bulb and apodeme (♂).

(Scale lines 0.1 mm.)

by fusion of the basimeres anteriorly over the dorsum of the andrium, thus forming a periandrium as in *Cyclorrhapha*. The groups which show such a periandrium (see figs. 6 and 7) have been suggested on other grounds as related to the *Cyclorrhapha* (implying that the "Empididae" is a paraphyletic group) by some recent authors. These suggestions are reviewed below in section 4.

Black (1966) describes the formation of the "epandrium" in *Eucalliphora* (Tachinidae s.l.) by growth of the evaginated lateral papillae of the ventral genital disc, which eventually fuse across the centre of the dorsum. My interpretation of the so-called "epandrium" of *Cyclorrhapha* as a periandrium formed from the basal articles of the parameres is thus fully compatible with the ontogenetic evidence. In conformity with this interpretation I reject Black's homology of the anterior papillae of the genital disc with the parameral lobes in Snodgrass' sense (= primary phallic lobes). I suggest that both the anterior and lateral papillae are divisions of the true parameral lobes, which should be sought in the larval stage (as in the nematoceros groups studied by Abdul Nasr). See section 6.1 for further discussion of the imaginal discs.

The periandrium usually bears a pair of articulated lobes which function as claspers during copulation. These have most commonly been called "surstyli" by recent authors. Other frequently used synonyms include "valvulae laterales" and "paralobi". If my view that the periandrium is formed from the basal articles of the parameres is accepted, then clearly these lobes may be accepted as their distal articles, for which Snodgrass (1957) has proposed the term telomeres (equivalent to the "dististyli" of many authors). Their formation as lobes of the developing lateral papillae of the genital disc described by Black (1966) fully accords with this

interpretation. In some Cyclorrhapha additional lobes are differentiated from the periandrium, or the telomeres are divided. I do not agree with Steyskal's (1957a) view that such conditions indicate that the "epandrium" is composed of fused 9th and 10th terga. In those groups in which discrete 9th and 10th terga are present (for instance the Rhagionidae), these are usually simple plates which do not bear articulated lobes. Only in certain Asilidae are more or less articulated lobes of the epandrium present (for which the name "surstyli" may appropriately be retained). However Karl's (1959) analysis indicates that the presence of surstyli cannot be ascribed to the groundplan of the Asilidae, and such conditions therefore do not indicate the character sequence leading to the conditions shown by Cyclorrhapha. It is interesting that Brundin (1966: 80) concluded that in "the basic design of the Nematoceros Diptera" (by which he must mean the groundplan of the Diptera as a whole, since the Nematocera are not a monophyletic group), the telomeres were double and articulated separately with the basimeres. Thus, even if the presence of double telomeres is a groundplan condition for the Cyclorrhapha, rather than secondary in this group as Hennig (1936a) maintained, no special difficulty need arise in interpreting this condition. However I think Hennig's interpretation more probable, as double or divided telomeres are only found in a few families of Cyclorrhapha.

Snodgrass (1935) stated that "movable claspers that can be identified with the harpagones, or styli of the gonopods, are absent in muscoid Diptera, but the 9th tergum commonly bears on its lower posterior angles a pair of long lobes, which may be flexible at their base but are not provided with muscles". Snodgrass' opinion was probably based on the morphology of *Pollenia* (Tachinidae s.l.). In that family movement of the telomeres

is produced by contraction of muscles inserted on the processus longi, not on the telomeres themselves, as has been confirmed by Salzer's (1968) detailed studies on *Calliphora*. However the condition shown by the Tachinidae s.l. is clearly apomorphous and not a general condition of the Schizophora ("muscoid Diptera"), as Snodgrass assumed. Certainly in some groups of Cyclorrhapha muscles are inserted on the base of the telomeres, for instance muscle "3" in Hennig's (1936a) description of the musculature of *Calycopteryx* (Micropezidae). Rivosecchi (1958) has described muscles inserted on the telomeres in *Musca* (Muscidae). I have also noted muscles inserted on the base of the telomeres in serial sections of a specimen of a *Syrphus* species (Syrphidae).

In most Cyclorrhapha the integument is strongly infolded between the sides of the periandrium above the base of the aedeagus, thus forming what may be called the periandrial fold. Sclerites linking the hypandrium and telomeres are often present in the upper wall of this fold. For a single such sclerite I propose the new term interparameral sclerite. The use of the term "10th sternite" for such a sclerite is clearly unwarranted, since the 10th segment is part of the proctiger, which lies above the telomeres. In some groups the sclerotization of the upper wall of the periandrial fold consists of a pair of lateral rod-like sclerites, known as the processus longi or bacilliform sclerites. It is possible that the processus longi of some Calyptratae arose as apodemes from the base of the telomeres, since they bear muscles apparently homologous with those inserted on the base of the telomeres in other groups (see preceding paragraph). The lower wall of the periandrial fold above the aedeagal apodeme is usually membranous, but sclerotization is developed here in a few groups (e.g. Micropezoinea).

The cyclorrhaphous hypandrium in my view consists solely of the 9th sternum and is fully homologous with the hypandrium of the Empididae (Orthogenya). In conformity with my conclusion that the periandrium is formed from the basimeres, I cannot accept suggestions that these may have been involved in the formation of the hypandrium. Chillcott's (1958) homology of the hypandrium with the basimeres (which he called "gonocoxites") was based on direct comparison with the condition in the Bombyliidae, where the basimeres and telomeres are ventrally situated and a true epandrium retained. While Chillcott's assumption that the conditions of the genitalia shown by the Bombyliidae are relatively plesiomorphous for the Brachycera seems substantially correct, he failed to consider the conditions shown by the Empididae, whose study is in my opinion essential to an understanding of the character sequences leading to the organization of the genitalia in Cyclorrhapha. Gooding and Weintraub (1960) tentatively suggested that the hypandrium may include elements derived from the preceding segments, because of the presence of a partial transverse suture in *Hypoderma*. However neither my comparative studies nor Black's ontogenetic studies provide evidence for such a fusion. Hennig (1936a) also suggested that the hypandrium was formed by fusion of two sclerites, but subsequently abandoned this view; van Emden and Hennig (1956) accepted the hypandrium as the 9th sternum.

The anterior end of the hypandrium is in some species produced into a rod-like process called the hypandrial apodeme. Posteriorly the hypandrium usually divides into a pair of hypandrial arms. In some groups these arms bear more or less vertically directed extensions posteriorly (called the vertical sections of the hypandrial arms in my descriptions).

My interpretation of the origin and homology of the hypandrium,

periandrium and telomeres (which for brevity may be referred to as the "periandrium hypothesis") may at first seem improbable, because it breaks with tradition. But it has much greater explanatory power in terms of the available evidence than the traditional view that the parameres (or "gonopods") have been lost or fused with the hypandrium, and that the large dorso-lateral sclerite represents an epandrium from which secondary appendages ("surstyli") are differentiated. The following points of comparison seem significant:

- (1) According to the periandrium hypothesis the clasping mechanism in the Cyclorrhapha does not differ substantially from that of many nematocerous families, and both the sclerites and some of the muscles involved may be homologized widely throughout the order Diptera. According to the traditional interpretation the sternal clasping mechanism (parameres) of the Nematocera and most non-cyclorrhaphous Brachycera has been lost and functionally replaced by secondary structures of tergal origin.
- (2) The periandrium hypothesis implies a gradual process of dorsal expansion of the basimeres, which is exemplified by the conditions shown by certain Empididae. The complete loss of the parameres which the traditional interpretation implies has not been supported by a convincing sequence of character change.

In the light of the above considerations I maintain that the periandrium hypothesis is much more consistent with the known facts and provides a simpler interpretation of them than the traditional homologies.

Pregonites and postgonites

In some Cyclorrhapha (see figs. 60 and 70) there are two pairs of lobes near the base of the aedeagus. Following Crampton and others I call

these the pregonites and postgonites. The homology of these structures has long been a source of difficulty. Either or both have often been called "parameres", a usage which Snodgrass (1957: 48) justifiably rejects. The postgonites are clearly a form of paraphysis, as there defined by Snodgrass. These are sensory lobes arising from near the base of the aedeagus; they are probably homologous with lobes present in certain Empididae and other "lower Brachycera", but the extent to which they can be homologized with similar structures in nematocerous families and other holometabolous orders has not been clarified. According to Black's (1966) study of *Eucalliphora* the pregonites (which she calls "anterior parameres") develop as lobes from the same papillae as the postgonites (anterior papillae 2). They thus represent additional paraphyses, not appendages of the hypandrium as some authors have suggested. Similar articulated pregonites are widespread among the Calyptratae, but the extent to which homologous structures occur in other groups of Cyclorrhapha is unclear. In some groups the structures which are called pregonites (or the equivalent) may in fact be processes or lobes of the hypandrium rather than paraphyses. My use of the term pregonites for groups other than Calyptratae is provisional, and does not indicate any firm opinion on homology. It has frequently been suggested that the pregonites of Calyptratae may be the distal articles of the parameres (the "styli of the gonopods" of van Emden and Hennig 1956), but this view cannot be reconciled with Black's account of their ontogeny.

Aedeagus

The intromittent organ itself I call the aedeagus, and regard the terms "phallus" and "penis" as synonyms. The aedeagus provides many characters which are important for the classification of the Schizophora.

In many Orthogenya the aedeagus is long and slender, more or less uniformly sclerotized, upcurved distally. I postulate below that an aedeagus of this type can be ascribed to the groundplan of the Eremoneura (see section 4). Among the Cyclorrhapha this type of aedeagus is shown by many Platypezidae (Platypezidea) and Lonchaeoidea (Schizophora) (figs. 21 and 23). In some Schizophora a complex mechanism has evolved for swinging the aedeagus about its articulation with the aedeagal apodeme into an anteriorly directed rest position. The groups which show this apomorphic condition are classified below in the Nothyboidea and Muscoidea. Salzer (1968) has described in detail the functioning of this mechanism in *Calliphora erythrocephala* Meigen (Tachinidae s.l.) (figs. 52 and 53), in which the arc of movement is about 160° . In other superfamilies of Schizophora (Lonchaeoidea, Lauxanioidea and Drosophiloidea) and in all non-schizophorous Diptera, only a limited degree of movement of the aedeagus in relation to the aedeagal apodeme is possible.

In those groups of Schizophora in which this swinging mechanism is present (Nothyboidea and Muscoidea), the walls of the aedeagus are differentiated into sclerites and membranous areas. The basal sclerite on which muscles are inserted is called the phallopore (= basiphallus). This is a large cylindrical structure in some groups, but in others consists of only a narrow basal ring or partial ring of sclerotization. The term "theca" recommended by van Emden and Hennig (1956) was originally applied by Wesché (1906) throughout the Diptera to structures of several different origins, and is clearly inappropriate in this context since it literally means a "sheath". Some authors have suggested that the term aedeagus or phallus should be restricted to parts distal to the phallopore. I follow van Emden and Hennig in rejecting this usage, because only the

whole intromittent organ can be widely homologized; the distinction between a phallopore and "aedeagus" in the above sense cannot be applied satisfactorily in groups other than Muscoidea and Nothyboidea. Metcalf (1921) considered the hypandrium and aedeagal apodeme of Syrphidae as parts of the "penis", and some of the terms used for the hypandrium by other authors on Syrphidae ("inner copulatory organ", "phallosome", "penis sheath") are also open to the misunderstanding that this is part of the intromittent organ. Such terminology is in my opinion misleading and should not be used. I apply the term paraphalli to lateral sclerites in the walls of the aedeagus of Muscoidea (see my characterization of that group below). In some groups of Muscoidea the phallopore bears a characteristic sclerotized fold or process which extends posteriorly from the base of the aedeagus. This is known as an epiphallus (= spinus). The epiphallus moves with the aedeagus when this is swung about its articulation with the aedeagal apodeme into the copulatory position. It is likely that an epiphallus has been evolved independently in different groups of Muscoidea.

Aedeagal apodeme and ejaculatory apodeme

The aedeagal apodeme (or phallapodeme) is usually a conspicuous structure articulated with the base of the aedeagus; it bears strong musculature involved in the extrusion and retraction of the aedeagus. Ontogenetically the aedeagal apodeme develops as an ingrowth of the integument at the base of the aedeagus (Schröder 1927, Black 1966). Hennig's (1958: 539-540) statement that the aedeagal apodeme "has a similar morphological value" to the epiphallus, because both structures represent sclerotized folds of the integument, is correct as regards their ontogeny, but these structures are not functionally equivalent. I suggest that in the groundplans of the

Syrphidea and Schizophora the aedeagal apodeme was rod-like (bacilliform), attached to the body wall only where it articulates with the base of the aedeagus. This condition is shown by all Syrphidea, as far as I am aware, and by many groups of Schizophora. The presence of any sclerotized link or fusion between the aedeagal apodeme and the hypandrium or body wall between the hypandrial arms, is treated as an apomorphous condition in my analysis. Such conditions occur widely among some groups of Schizophora, and have probably been evolved independently on many occasions.

The ejaculatory apodeme (fig. 8) is a completely internal apodeme, arising from the wall of the ejaculatory duct. It serves as the attachment for muscles which force seminal fluid from the ejaculatory bulb (an expanded chamber of the ejaculatory duct) through the narrow terminal part of the duct. Although an internal structure, this apodeme is conveniently considered together with the external genitalia, as it is ectodermal in origin and can be readily studied in macerated preparations. Such an apodeme occurs in all Syrphidea and Schizophora, except where secondarily reduced.

Further investigation is needed to clarify the homologies of the aedeagal apodeme and ejaculatory apodeme of Cyclorrhapha with structures found in other Diptera. Hennig (1936a) suggested that both these apodemes may have arisen by splitting of a previously uniform structure equivalent to the "ejaculatory apodeme" of Orthogenya, but no convincing evidence supports this hypothesis. An alternative explanation is that the "ejaculatory apodeme" of Orthogenya is homologous with the aedeagal apodeme of Cyclorrhapha, and that the ejaculatory apodeme of some Cyclorrhapha (Syrphidea and Schizophora) is neomorphous. Two criteria can be adduced in support of the interpretation that the aedeagal apodeme of Cyclorrhapha

is homologous with the "ejaculatory apodeme" of *Orthogenya*: similarity of position and similarity of musculature. Both structures articulate with the base of the aedeagus, and hence occupy a similar position in relation to other hypopygial structures; and according to Trehen's (1960, 1962) studies the muscles of the "ejaculatory apodeme" of Empidinae all insert on the hypandrium or at the base of the aedeagus, as is the case with the cyclorrhaphous aedeagal apodeme. However, this interpretation conflicts with another valid criterion of homology, continuity of function; for it involves postulating that the ejaculatory function has been lost by one structure and taken over by a neomorphous structure. I think any conclusion must await detailed comparative information on the structure of the Platypezidea and Hypocera. In two species of Platypezidae, *Polyporivora polypori* (Willard) and *Plesioclythia agarici* (Willard), I have found sclerotized areas and musculature on the terminal part of the ejaculatory duct; but the conditions are very different in each case, and it is not clear whether either is relevant to the evolution of the characteristic ejaculatory bulb and apodeme of Syrphidea and Schizophora.

Proctiger

The proctiger, containing elements derived from the 10th to 12th segments of primitive insects, is usually much reduced in the Cyclorrhapha. The 10th tergum seen in Rhagionidae (fig. 5), like the 9th tergum, seems completely lost. The only large sclerotized structures are the cerci. Some authors have maintained that these are not cerci but should be called "paraprocts" or "parapodial plates". However, Herting (1957) has pointed out that in the groundplan of the Brachycera these structures are biarticled in the female, which supports the view that they are true cerci. The homology of the male and female structures has been demonstrated by Milani

and Rivosecchi (1955), who have described a convincing series of intermediate conditions from sexually abnormal specimens of *Musca domestica* L. The 10th sternum (on the ventral side of the proctiger) is vestigial or absent in many Cyclorrhapha, but is distinct in the hypoceran *Ironomyia* figured by J. F. McAlpine (1967) (as "? sternite 11").

The meaning of such terms as "dorsal", "ventral", "left" and "right" is potentially ambiguous because parts of the male postabdomen of Cyclorrhapha are rotated and deflexed (as explained in detail in section 3.2). I disregard the effects of rotation in applying these terms, so that, for instance, the large inverted 8th sternum is described as occupying a "dorsal" position. However deflexion of the hypopygium must be taken into account in interpreting my use of such terms as "dorsal" and "ventral". Thus the cerci and the centre-line of the periandrium are always considered to indicate the "dorsal" side of the hypopygium, irrespective of the degree of deflexion.

3.2. The "*hypopygium circumversum*" condition

The subject of hypopygial circumversion (rotation through 360°) in male cyclorrhaphous Diptera has attracted much interest and comment over the years, although few authors have attempted to discuss all the extensive pertinent literature. Perhaps the most balanced previous review is that in Lindner's (1949) handbook in "Die Fliegen der paläarktischen Region". Very recently the subject has acquired a new dimension as the result of discoveries made by E. L. Kessel of the University of San Francisco in the course of his studies on Platypezidae (Kessel and Maggioncalda 1968, Kessel 1968). These discoveries provide the first important new factual

information on this subject since the 'thirties.

Confusion has long persisted in the literature because of the widespread currency of theories which assume some direct causal relationship between hypopygial circumversion and the asymmetrical conditions of the postabdomen shown by the Muscoidea (in the sense defined below). The most influential source of such theories was G. C. Crampton. Hennig (1958) criticized some aspects of Crampton's views, but several other authors have continued to accept them in their entirety. In view of this continuing controversy, I think that progress will be best served if I include here a critique of the views of Crampton and G. H. Hardy, who approached this question with similar assumptions.

The evidence for circumversion

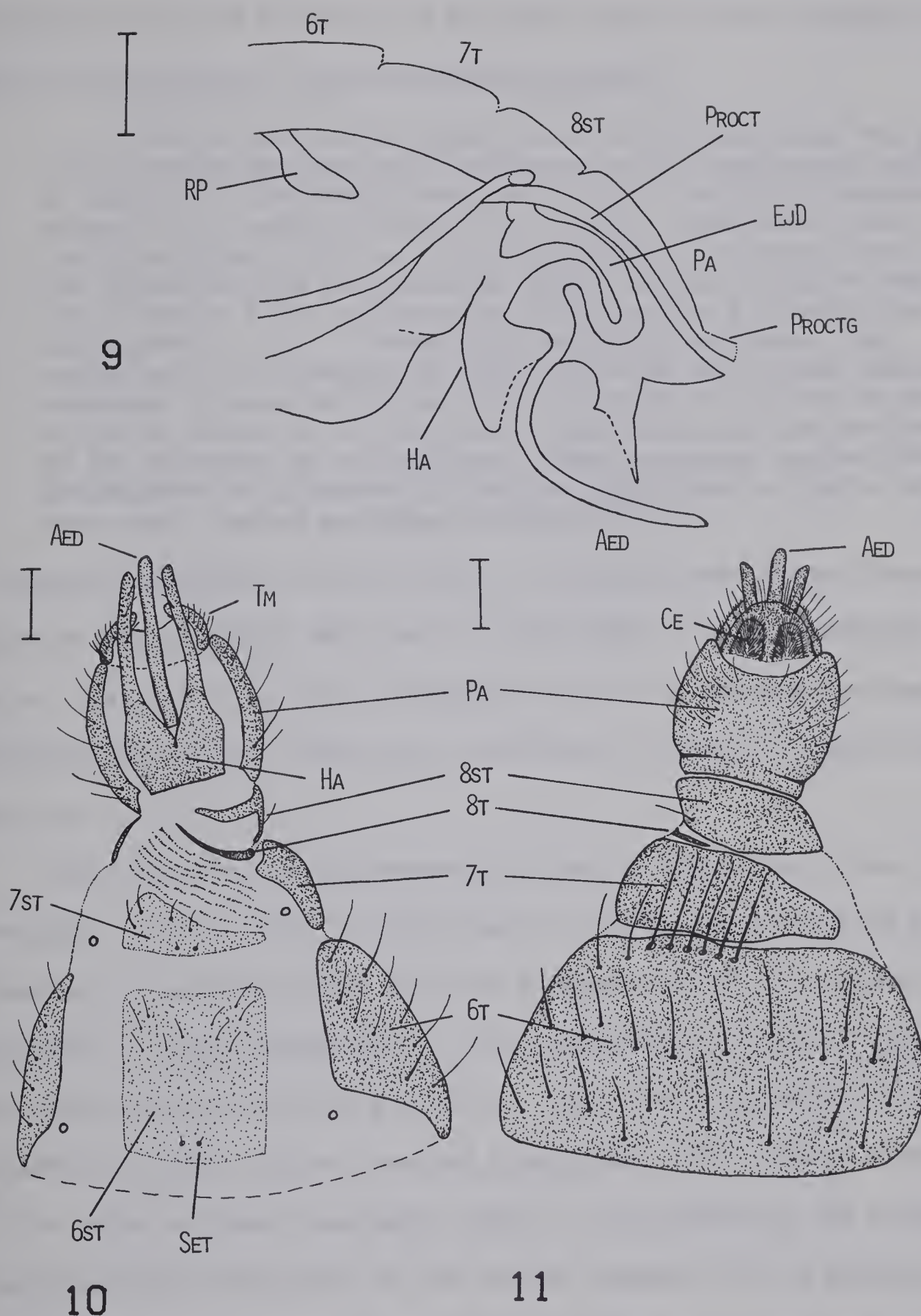
Feuerborn (1922) proposed the term "*hypopygium circumversum*" in the sense of a rotational circumversion of the hypopygium. He did not observe the rotation, but postulated its occurrence inside the puparium of *Calliphora* to explain the looping of the ejaculatory duct over the hind gut in this genus (to which Brüel [1897] had first drawn attention). Feuerborn's conclusion was fully confirmed by the work of his pupil Schröder (1927), who demonstrated that in *Calliphora* a 360° clockwise rotation of the hypopygium took place on roughly the fifth day after pupation. Schröder thought that the duration of the process was at most 24 hours. He claimed that a growth process was responsible for the rotation, since he could see no muscles in his serial sections.

Gleichauf (1936) published a detailed study of the development of *Drosophila melanogaster* (Meigen). He concluded that circumversion began on the second day after pupation, and was completed at latest by the end of the third day. The direction of the rotation was clockwise, as in *Calliphora*.

Further observations on the process of circumversion within the puparium are found in recent works by Milani and Rivosecchi (1955), referring to *Musca domestica* L., and Gooding and Weintraub (1960), referring to *Hypoderma* spp. These accounts are less detailed than the earlier works, but clearly indicate the occurrence of rotation within the puparium, as described for *Calliphora* and *Drosophila*.

The process of circumversion has certain characteristic effects upon the internal structure of the mature adult. First, the ejaculatory duct is looped over the hind gut, passing upwards on the left side of the insect, then crossing above the gut, and then passing downwards to the aedeagus on the insect's right side (fig. 9). Both Schröder and Gleichauf demonstrated that this looping resulted directly from the rotation of the hypopygium within the puparium, this vindicating Feuerborn's (1922) hypothesis. Secondly, the postabdominal nervous system shows a double chiastoneury (crossing over) of the *nervi terminales*, as Salzer (1968) has described in much detail. Thirdly, the longitudinal tracheal trunks are crossed posterior to the last pair of spiracles (fig. 12).

As far as is known, the process of circumversion is completed within the puparium in all Schizophora. But Kessel and Maggioncalda (1968) and Kessel (1968) have reported that in certain Platypezidae only the first 180 degrees of the rotation takes place within the puparium; the additional 180 degrees takes place in the teneral state immediately following emergence. The extent to which muscular action is involved in the first part of rotation within the puparium has not been investigated; but it is evidently involved at least in the part of rotation completed after emergence. Kessel and Maggioncalda state that all the movements involved in the post-emergence part of circumversion in platypezids occur to the right



Figs. 9 - 11. 9. *Plesioclythia agarici* (Willard) (♂) (Platypezidae), schematic representation of the ejaculatory duct and hind gut, with an outline of the body wall as seen in sagittal section along the mid-line. 10. *Plesioclythia agarici* (Willard), postabdomen in ventral view of mature male, showing a *hypopygium circumversum* condition. 11. *Plesioclythia agarici* (Willard), postabdomen in dorsal view of mature male, showing a *hypopygium circumversum* condition.

(Scale lines 0.1 mm.)

of the main axis of the body; in the most teneral flies examined (of the genus *Plesioclythia*), the postabdomen projected

"... sharply out to the right in the horizontal plane and a little toward the rear with reference to the longitudinal axis of the body. The seventh and particularly the eighth abdominal segments are somewhat attenuated to form a stalk which bears the hypopygium at its end. The hypopygium is inverted, with the hypandrium and its parameres above, and the epandrium and its surstyles below, showing the circumversion has progressed 180 degrees Immediately following emergence, the second half of circumversion takes place as the stalked abdomen continues to move in its arc, rotating another 180 degrees as it passes downward and posteriad to finally reach the position of its beginning at the midline. These movements complete the 360 degrees of circumversion and the hypopygium is right-side-up once more" (Kessel and Maggioncalda 1968: 82).

A similar description of the process in *Paraplatypeza coraxa* (Kessel) is given by Kessel (1968: 246), with a photograph of a newly emerged living male. Plates I and II are photographs of a newly emerged specimen of *Plesioclythia agarici* (Willard), from material which Dr. Kessel kindly sent me.

The completion of circumversion in such Platypezidae is not irreversible. Kessel (1968) reports that all Platypezidae which he has observed in copulation have utilized a linear position (or rather "opposed position", if one follows Hardy's 1944 definitions), that is "tail-to-tail and right-side-up for both partners". Such a mating position can only be expected in flies with an inverted hypopygium, since inverse correlation of the male and female genitalia (that is, the dorsum of the aedeagus contiguous with the venter of the vagina) appears to be a mechanical necessity in insects, with the probable exception of some Lepidoptera and Trichoptera (Richards 1927, Hardy 1944). A mount of a mating pair of *Grossoseta californica* (Kessel), a unique mount since platypezid pairs usually separate on capture, confirms that the male hypopygium is in an

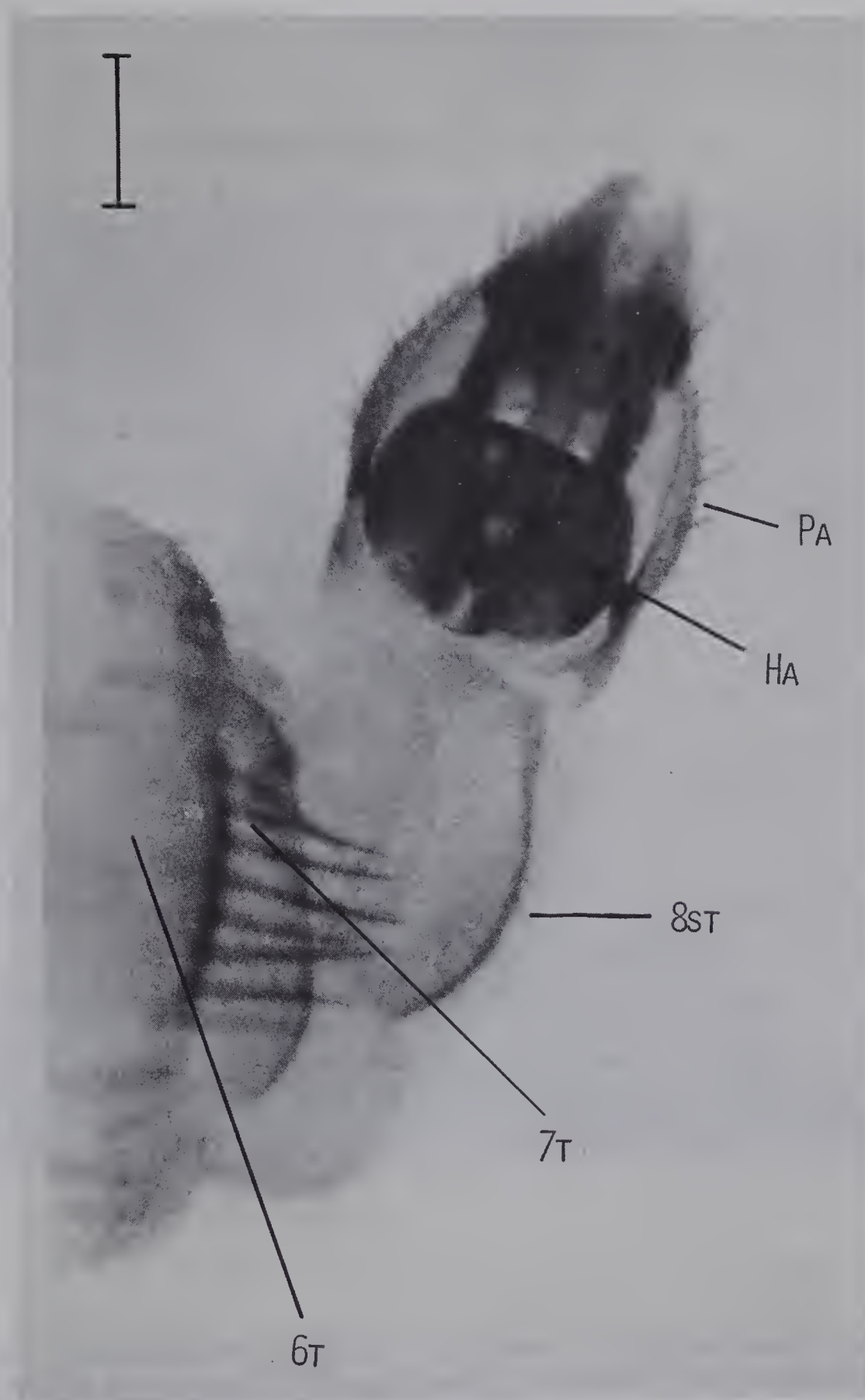


Plate I. *Plesioclythia agarici* (Willard) (Platypezidae), postabdomen in dorsal view of newly emerged male, showing a *hypopygium inversum* condition (photograph by Dr. D. A. McB. Craig).

(Scale line 0.1 mm.)

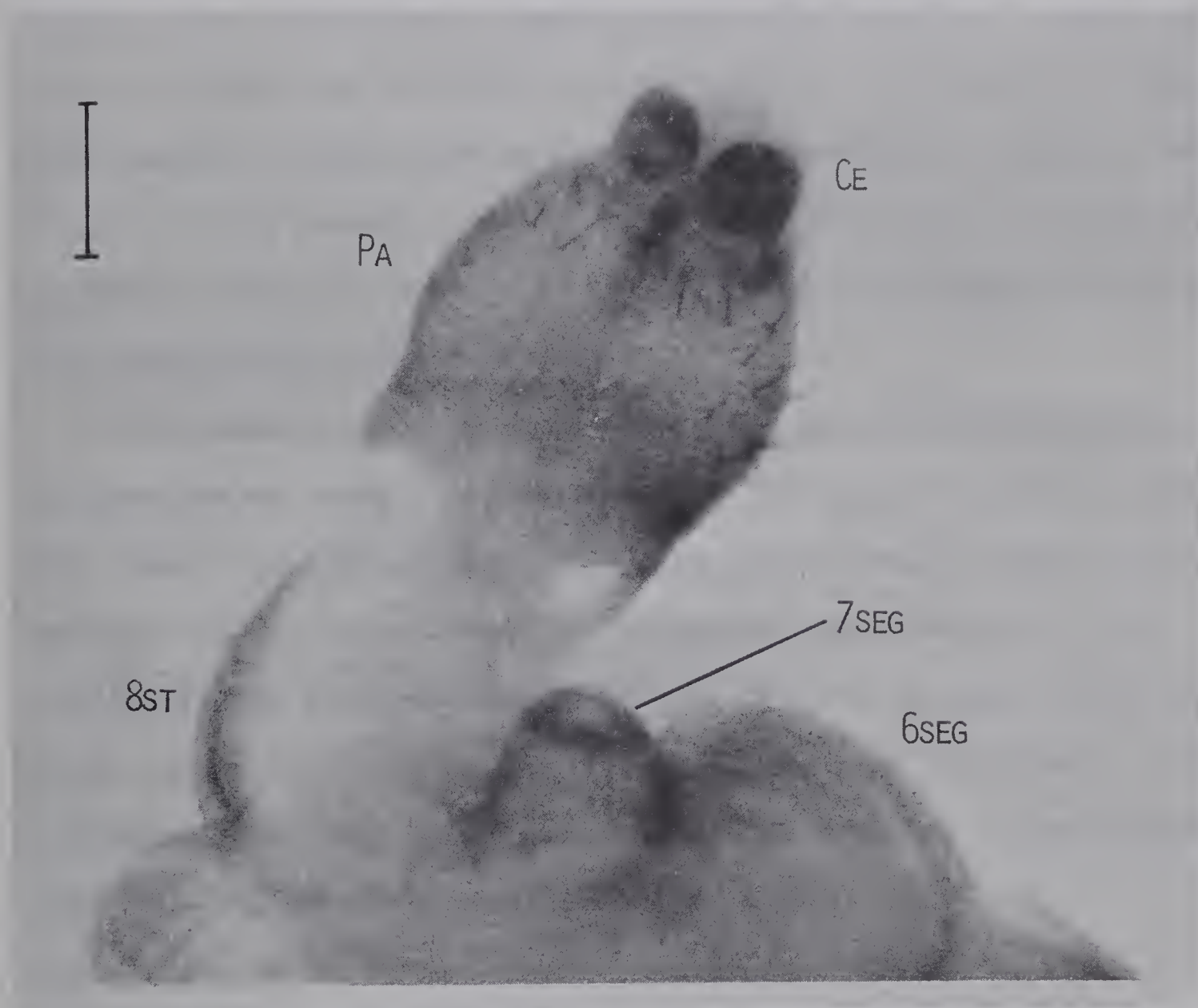


Plate II. *Plesioclythia agarici* (Willard) (Platypezidae), postabdomen in ventral view of newly emerged male (the same individual as shown in plate I) (photograph by Dr. D. A. McB. Craig).

(Scale line 0.1 mm.)

inverse position. Kessel has concluded that the hypopygium was unwound (anticlockwise) through 180 degrees from the circumverse to the inverse position. I have seen the mount in question and agree with this interpretation. Opposed mating positions are, for obvious reasons, normally assumed after copulation has begun in some other position. Kessel has not yet observed how copulation in platypezids is initiated, but suggests that the male vertical pose (a "superimposed position" in Hardy's terminology) is first assumed, with the male hypopygium still in the circumverse position. However this needs to be confirmed by observation, as there are other possibilities (see Hardy 1944).

The process of reversible circumversion now established for the Platypezidae may clearly be regarded as a less modified condition than that shown in the Schizophora, where the entire process occurs within the puparium and is irreversible. The change which has occurred is the acceleration of an ontogenetic process, so that it is completed at an earlier stage in relation to the overall ontogeny of the animal. It has unfortunately not been made clear whether the insect is a pupa or pharate adult when rotation takes place in Schizophora.

Distribution of the "hypopygium circumversum" condition

While the number of species for which circumversion has been demonstrated directly in ontogenetic studies is very low, the occurrence of circumversion can also be inferred from looping of the ejaculatory duct over the hind gut. Since looping of the ejaculatory duct over the hind gut has now been confirmed for a representative range of species, I am confident that the *hypopygium circumversum* condition is universal among male Cyclorrhapha, and that the more plesiomorphous reversible expression of this character

shown by the Platypezidae occurred in the last common ancestor of the group. Table 1 sets out in detail the evidence for making such a generalization.

The information on the distribution of circumversion is still inadequate in some respects. In particular, no detailed information is available on the process of circumversion and mating positions in the Lonchopteridae. The only relevant information is Hennig's (1958: 535) brief statement to the effect that he thought he saw looping of the ejaculatory duct over the hind gut in *Lonchoptera* ("*Musidora*"). In view of the postulated sister-group relationship between the Lonchopteridae and other Cyclorrhapha (see section 5), investigations on circumversion, mating positions and related questions in this family might yield interesting results from an evolutionary point of view. The other major gap in the information concerns the timing of the process of circumversion in the Hypocera and Syrphidea. I suspect that in the Syrphidea the process is completed at an early stage within the puparium, as in Schizophora, since the lack of extensive intersegmental membranes in the postabdomen of Syrphidea makes the possibility of rotation after the sclerites have been formed seem unlikely. But there have been no ontogenetic studies which clarify this point.

Loss of circumversion has not been demonstrated in normal males of any species of Cyclorrhapha, although abnormal specimens with only partial rotation of the hypopygium are known in *Drosophila* (extensive literature) and *Musca* (Milani and Rivoecchi 1955). In the micropezid *Calycopteryx moseleyi* Eaton from Kerguelen Island the rotation has been reduced to about 320° (see Hennig 1936a); this is doubtless a secondary modification, since the normal 360° rotation occurs in other Micropezidae. Skaife's

Table 1. List of genera for which the *hypopygium circumversum* condition has been established by ontogenetic studies or by examination of the course of the ejaculatory duct in relation to the hind gut.

Acroptera

Lonchopteridae - *Lonchoptera* (Hennig 1958: 535)

Atriata

Platypezidea

Platypezidae - *Calotarsa** (Kessel & Maggioncalda 1968),
*Plesioclythia** (Kessel & Maggioncalda 1968), *Polyporivora***

Hypocera

Phoridae - *Anevrina***

Syrphidea

Pipunculidae - *Alloneura***

Syrphidae - *Syrphus* sens. lat.**, genus not stated (van Emden 1951)

Schizophora

Lauxaniidae - *Sapromyza* (Hahn 1929), *Lauxania***

Chamaemyiidae - *Chamaemyia***, *Leucopis***

Drosophilidae - *Drosophila* (Gleichauf 1936, Miller in Demerec 1950, etc.)

Ephydriidae - *Scatophila* (Bolwig 1940), *Psilopa***

Psilidae - *Loxocera***

Micropezidae - *Micropeza* (Hennig 1934)

Sciomyzidae - *Pherbellia***

Sepsidae - *Nemopoda***

Sphaeroceridae - *Leptocera* sens. lat.**

Trixoscelididae - *Zagonia***

Anthomyzidae - *Anthomyza***

(Cont'd)

Table 1 (Cont'd)

Clusiidae - *Clusia***

Agromyzidae - *Melanagromyza** (Ipe 1967), *Phytomyza***

Chloropidae - *Chlorops***

Conopidae - *Thecophora***

Tephritidae - *Dacus*, *Chaetostomella* and *Urophora* (= *Euribia*)
(Hennig 1936a), *Tephritis* (Rivosecchi 1957)

Anthomyiidae - genus not stated (Chillcott 1958)

Muscidae - *Musca* (Hewitt 1907, Milani & Rivosecchi 1955,
Rivosecchi 1958), *Stomoxys* (Tulloch 1906)

Hippoboscidae - *Raymondia* (Jobling 1951), "Nycteribiidae"
(genus not stated) (Theodor & Moscona 1954a)

Glossinidae - *Glossina* (Minchin 1905, Zumpt 1936)

Tachinidae - *Calliphora* (Brüel 1897, Schröder 1927, Richards
1927, Salzer 1968), *Phormia* (Crampton 1944a), *Ernestia*
(Petzold 1927), *Hypoderma* (Mote 1929, Gooding & Weintraub
1960)

*The single asterisk indicates that the published record has been confirmed by examination of serial sections of the abdomen in my possession.

**The double asterisk indicates a new record based on serial sections of the abdomen in my possession.

(1921) account of the internal reproductive system of *Braulā* (Braulidae) does not include reference to looping of the ejaculatory duct over the hind gut, which is surprising as there seems no doubt that *Braulā* is a true schizophoran. However Skaife's description is very brief, and I suspect that his observations were incomplete. Unfortunately I was unable to obtain fresh material of *Braulā* to check this point. Ferris (in Demerec 1950: 418) published some remarks which cast doubt on the occurrence of rotation in *Drosophila*, and several later authors have cited these. However, Ferris seems to have been unaware that circumversion in *Drosophila* had been conclusively demonstrated by Gleichauf (1936), since he makes no reference to that paper.

Direction of rotation

Rotation normally occurs in a clockwise direction (as seen from behind) in all species investigated.

Milani and Rivosecchi (1954, 1955) described a "countercoiled" mutation in *Musca domestica* L. in which the hypopygium is rotated in an anti-clockwise direction, and referred to the existence of a similar mutation in *Drosophila* (Milani and Rivosecchi 1955: 347). These authors concluded that in *Musca* the mutation was highly disadvantageous because of imperfect integration with the rest of the genome, and occurred only at frequencies in the order of magnitude of 1:10,000 in natural populations.

Which segments are involved in rotation?

Circumversion clearly involves the whole hypopygium, that is the 9th (genital) segment and the proctiger, including the hypandrium, which ontogenetic studies have shown to be wholly derived from the 9th segment. But difficulties have arisen in judging to what extent segments preceding the hypopygium are involved. Some authors (notably Crampton, Aczél and

G. H. Hardy) drew conclusions from the strongly asymmetrical structure of the postabdomen in some groups, in particular the Syrphidea and Muscoidea. But this reasoning is clearly unwarranted, as the asymmetries in question are not present in the groundplan of the Cyclorrhapha and have not been shown by ontogenetic studies to be the result of rotation. My views in this respect accord fully with those expressed by Hennig (1958) in criticizing the work of Crampton. In the groundplan of the Schizophora the 6th and 7th abdominal segments were more or less unmodified, with terga and sterna in normal dorsal and ventral positions (as also in the Platypezidae); the *hypopygium circumversum* condition must therefore have evolved long before the asymmetrical conditions of the sclerites of the 6th and 7th segments with which it has been causally linked by Crampton, Hardy and others. In view of the above considerations, I reject all conclusions based on inferences from the arrangement of the sclerites of the mature adult, and proceed first by considering whether there is ontogenetic evidence for rotation of segments preceding the hypopygium in the Schizophora. Relevant information is given by Schröder (1927) and Gleichauf (1936). After considering the evidence for Schizophora (on which the views of earlier authors were largely based), I then support my argument with the new information now available on circumversion in the Platypezidae (Kessel and Maggioncalda 1968, Kessel 1968).

The point of rotation is well known for many "*hypopygium inversum*" forms belonging to nematocerous groups. But the point of rotation in the Cyclorrhapha cannot be reliably inferred from the conditions shown by such forms, since none can be synapomorphous in this respect with ancestors of the Cyclorrhapha. The most closely related groups to the Cyclorrhapha (the Orthogenya and other groups of Brachycera) consist, with few exceptions,

of species without hypopygial rotation. Feuerborn (1922) and several subsequent authors seem to have assumed that the 180° rotation shown by certain nematocerous groups was an ancestral condition leading to the 360° rotation of Cyclorrhapha. But this view cannot be reconciled with modern conclusions on the phylogeny of the Diptera.

Schröder (1927) demonstrated that the 6th sternum ("Basalring") in *Calliphora* takes no part in the rotation. It became visible before the start of the process and remained in unchanged position throughout. Unfortunately Schröder was unable to reach a firm conclusion on the extent to which rotation occurred in the area immediately preceding the hypopygium, which in *Calliphora* bears a large sclerite formed by partial fusion of elements derived from the 7th and 8th segments (called "7th tergite" by Schröder). The sclerotization of this area did not become distinct until rotation was almost completed. However his observations suggested that some degree of rotation probably occurred here.

Gleichauf (1936) concluded that in *Drosophila* the sclerites preceding the hypopygium were not rotated. This conclusion confirms Schröder's finding that the 6th segment is not rotated, and also rules out the possibility of rotation of the 7th segment (whose tergum is fused with the 6th tergum in male Drosophilidae). However his observations could not clarify to what extent the 8th segment might be rotated, as the sclerites of this segment are much reduced or absent in male Drosophilidae. When Gleichauf writes of rotation between the 7th and 8th segments, he means between the 7th segment and the hypopygium. He thought that the basal phragma of the periandrium represented the 8th tergum, but this is now known to be incorrect (see my treatment of the Drosophiloidea in section 6.2).

I think it must be accepted that Gleichauf's observations definitely rule out any involvement of the 6th and 7th segments in rotation, despite the speculation to the contrary by later authors, such as Hardy (1944). The view that the 7th segment is substantially rotated ("laterovered", that is turned through 90° , according to Crampton 1942) has not been supported by ontogenetic evidence. Furthermore, the pattern of sclerotization on which Crampton's and other similar views have been based is an apomorphous condition confined to part of the Schizophora (the Muscoidea in the sense proposed in this work), and not a condition of the whole of the Schizophora, as Crampton seemed to assume.

Munro (1947) suggested that in *Calliphora* the spiracles of the 7th segment "will have reversed their positions, and the right spiracle of the synsternite will have come to lie next to the sixth spiracle of the left side". Kim and Cook (1966) suggested that one of the postabdominal spiracles is carried to the other side of the body in Sphaeroceridae. But these suggestions are contrary to the evidence. Rivoecchi's (1958: 480) figure of the tracheal system of *Musca domestica* L. (copied here as fig. 12) shows clearly that the lateral tracheal trunks are only crossed posterior to the spiracles of the 7th segment. The same is the case with every other cyclorrhaphan whose tracheation has been examined. There are no grounds for postulating that any spiracles have crossed from one side of the body to the other.

To summarize, the ontogenetic work of Schröder and of Gleichauf clearly showed that the 6th and 7th segments are not rotated. Schröder's observations indicated that the 8th segment might be rotated, but he did not reach a firm conclusion. The argument between Crampton and his critics about whether the 8th segment is rotated through the full 360° or only

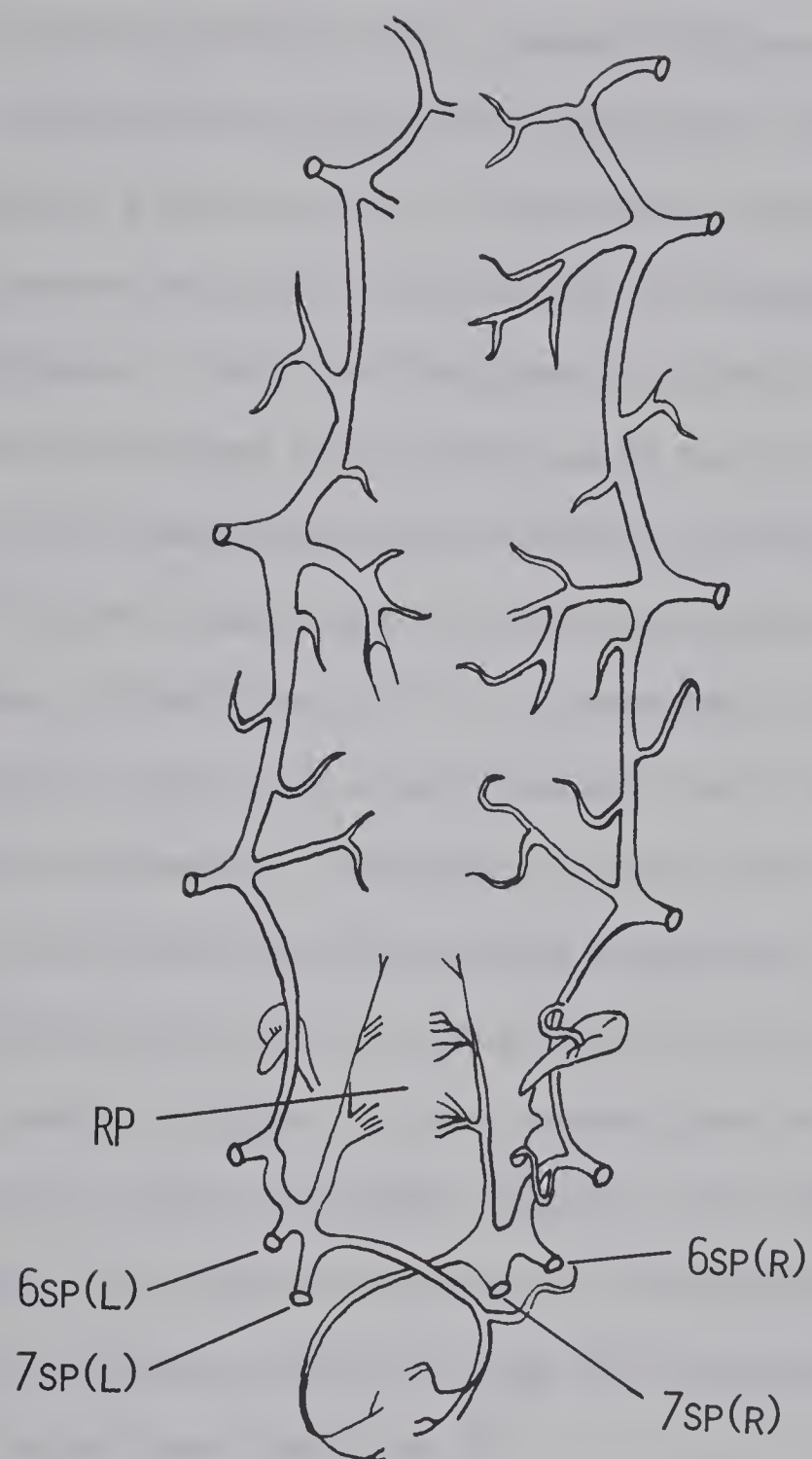


Fig. 12. *Musca domestica* L. (Muscidae), tracheation of male abdomen (after Rivosecchi 1958) (dorsal view).

through 180° was unresolvable at the time, since there was insufficient information upon which the question could be judged.

The new information on the process of circumversion in the Platypezidae (Kessel and Maggioncalda 1968, Kessel 1968) does not conflict with any of the conclusions on segmental involvement stated above; but it clarifies several points, since in Platypezidae all the abdominal segments are discrete and part of the process of circumversion takes place after emergence. Kessel and Maggioncalda (1968) originally believed that rotation began at the junction of the 6th and 7th segments (the junction of the preabdomen and postabdomen according to their definitions). This view was based on visual observation under the dissecting microscope of the final 180° of circumversion, which occurs rapidly (requiring no more than a few minutes) shortly after emergence of the fly from its puparium. Following the realization that the hypopygium is "unwound" to the inverse position during copulation, Kessel (1968) has somewhat modified his earlier view on the basis of study of the available mount of a pair *in copula*. He now reports that no rotation has occurred between the sixth and seventh segments, but that the part of the seventh segment after the 7th tergum is "considerably distorted" and "flattened by the pressures resulting from the progressively greater rotation of the structures distal to it".

It is pertinent here to consider the morphology of the terminal abdominal segments in *Plesioclythia agarici* (Willard), selected as a representative of the Platypezidae (figs. 10 and 11). Dorsally there is a complete series of eight sclerites before the periandrium, and ventral sterna of normal appearance continue as far as the 7th segment. These sterna bear *sensilla trichodea*, thus confirming Wheeler's (1960) conclusion

that the sensilla form a homonomous ("serially homologous") series as far as the 7th sternum. The 8th segment is largely membranous ventrally, but bears a band-like sclerite which extends from the venter around the right side of the insect, where it lies inside the apex of the 7th tergum.

It is clear from the structure of newly emerged males (plates I and II) that the definitive external structures of the 7th segment, namely the tergum, the sternum and the spiracles, are not rotated. The 7th segment is only involved in rotation to the extent that its membranous areas (especially of the venter) take up some part of the turn between the sclerites of the 7th and 8th segments. In *Plesioclythia* the ventral membranes after the 7th sternum appear involved in rotation to some extent, while the lateral membranes (where the 7th spiracles are situated) are not. These two areas of membrane are delimited in the specimen photographed (plate II): the swollen central area is continuous with the membrane of the 8th segment, and no clear intersegmental boundary is evident. Most of the first 90° of the observed post-emergence rotation of 180° occurs between the sclerites of the 7th and 8th segments. In newly emerged specimens (plates I and II) the large sclerite of the 8th segment lies on the left side of the insect, and only moves through 90° to its normal dorsal position as the hypopygium is moved through 180° (from the inverse to the circumverse position). The mount of the pair of *Grossoseta in copula* shows that the same differential rotation occurs when the hypopygium is unwound to the inverse position during copulation. The remaining 90° of the post-emergence rotation of 180° must therefore occur between the sclerites of the 8th segment and the hypopygium.

This observed differential rotation of the 8th segment indicates that this segment is not rotated through the full 360° . If the same differential

rotation occurs within the puparium as that observed after emergence (which seems to me the most probable hypothesis), then the 8th segment must be inverted when the hypopygium is in its circumverse rest position, as Crampton thought. Since I believe that the irreversible "*hypopygium circumversion*" condition of the Schizophora is a further development of the condition shown by the Platypezidae, I therefore homologize the large dorsal sclerite of the 8th segment present in some groups of Schizophora with the 8th sternum, and consider the band-like ventral sclerite (retained only in a few Schizophora) to be a reduced 8th tergum.

To summarize, I conclude that rotation in male Cyclorrhapha occurs between the hypopygium and the sclerites of the 8th abdominal segment, and between the sclerites of the 7th and 8th segments (with a slight involvement of part of the ventral membrane of the 7th segment); the sclerites and spiracles of the 7th segment are not involved in rotation. Differential rotation between the 8th segment and the hypopygium can be observed in adult platypezids, in which the last 180° of hypopygial rotation takes place after emergence from the puparium and is reversible. Ontogenetic studies on Schizophora (where the whole process of circumversion takes place within the puparium) give no reason to suppose that the segmental involvement differs from that observed in Platypezidae. The opinion of some authors that the 6th and 7th segments are rotated to some degree was based on the assumption that the asymmetrical conditions of the sclerites of these segments shown by certain groups were caused by rotation; this assumption is not supported by ontogenetic evidence. While it is not impossible that in some groups with a highly modified postabdomen, particularly the Syrphidea and Muscoidea, the process of circumversion has been modified to involve to a limited degree segments preceding the 8th, I think

it unwarranted to assume that this is the case in the absence of evidence. Asymmetrical sclerites may develop *in situ*, and this is always the simplest explanation in my opinion. In accordance with the principle of parsimony we should not assume that any unusual ontogenetic phenomenon such as rotation has occurred, unless there is positive evidence to this effect.

The views of G. C. Crampton

Crampton (1941, 1942, 1944a) propounded a theory in which various asymmetrical conditions of the postabdomen in Cyclorrhapha were explained as the direct result of circumversion. This theory still commands widespread support, in spite of the criticisms of van Emden and Hennig (1956) and Hennig (1958). Crampton's method was to place the conditions found in various families of Cyclorrhapha in an evolutionary series, leading from the "borderline" families Lonchopteridae and Phoridae, through the Syrphidea (Syrphidae and Pipunculidae), through various "acalyptrate" families, culminating in the conditions found in various Calyptratae. He claimed that the 7th segment in the Cyclorrhapha becomes "lateroverted" (turned through 90°) and the 8th segment inverted (turned through 180°) through involvement in the process of rotation.

I support Hennig's (1958) criticism of Crampton's theory, for the following reasons:

(1) Crampton's placing of conditions shown by certain Syrphidea in an evolutionary sequence leading to the conditions shown by the Calyptratae seems to me untenable, because the Syrphidea show in their groundplan apomorphous conditions of the postabdomen which are not present in the groundplan of the Schizophora (see also under section 5). According to my present analysis the diverse arrangements of postabdominal sclerites shown by various groups of Schizophora have been derived from a more or less

symmetrical condition of the type shown by the Platypezidae. If this view is correct, the condition shown by the Syrphidea must be considered an independent modification of the structure shown by Platypezidae, not a stage in a character sequence involving ancestors of the Schizophora.

(2) Crampton assumed that the asymmetrical arrangement of the post-abdominal sterna shown by the Muscoidea (in the sense of this paper) was a general condition of the Schizophora. My analysis indicates that this is incorrect, since there are a few groups of Schizophora in which both the 6th and 7th sterna are symmetrically developed in ventral position.

(3) No ontogenetic evidence supports Crampton's view that the 7th abdominal segment is "lateroverted" (rotated through 90°), as discussed previously in this section.

In one important respect I think that Crampton was correct: this is that the 8th segment is inverted and bears its sternum in dorsal position. However, at the time Crampton wrote there was no convincing evidence to prove that he was correct, and it is understandable that many authors, including Hennig, were sceptical.

After publication of his theory Crampton attempted a wider study of the terminalia of the so-called "Acalyptratae", but never published his results in detail. He produced a "purely tentative arrangement" of some families of "Acalypterates" (Crampton 1944b), but this paper contained only the briefest characterization and has had little influence on subsequent workers. It was strongly criticized by Hennig (1958). Crampton classified the "Acalypteratae" (in which he included the Syrphidae, Pipunculidae and Platypezidae, as well as the customary range of schizophoran families) into two divisions, the "Syrphomorpha" and "Platypezomorpha", on the basis of the sclerites of the 6th abdominal segment. Such a classification cuts

right across all other evidence; it was a logical consequence of his assumption that the conditions of the terminalia found in the Syrphidae and Pipunculidae were a stage leading to the evolution of the asymmetrical conditions of the groups which I classify as Muscoidea. Groups whose structure conflicted with this assumption because they showed an obviously more plesiomorphous condition of the 6th segment, were assumed to belong to a different evolutionary line, and were therefore classified in the highly heterogenous assemblage "Platypezomorpha".

The views of G. H. Hardy

Hardy (1944) published a useful analysis of copulating positions in Diptera, but unfortunately his speculation in that paper regarding the origin of the "*hypopygium circumversum*" condition is misleading. Hardy seems to have been unaware of Schröder's (1927) and Gleichauf's (1936) ontogenetic studies which conclusively proved the correctness of Feuerborn's (1922) hypothesis of rotational circumversion in the Cyclorrhapha; instead he elaborated a theory which purported to show that Feuerborn's conclusion was a misunderstanding, and that the observed looping of the ejaculatory duct over the hind gut in *Calliphora* indicated a "*hypopygium inversum*" condition. The condition shown in Syrphidae was considered to be a stage from which that of the Calyptratae was derived by movement of the anus. In support of this remarkable suggestion he argued that "authors had overlooked the fact that the aedeagus had remained inverted in an apparently erect hypopygium".

The evolutionary series constructed by Hardy is clearly contrary to the available evidence. His suggestion that the condition found in Syrphidea had originated by "curving round" of a *hypopygium inversum* is contradicted by the evidence now available that the *hypopygium circumversum*

condition (in its partly reversible expression) was already present in the groundplan of the Cyclorrhapha. I have explained above (in the discussion of Crampton's views) why I do not think that the condition found in Syrphidea is similar to that of any ancestor of the Schizophora. Hardy's generalization that the aedeagus is "inverted" (directed anteriorly rather than posteriorly) in Schizophora (called "Muscoidea" by Hardy) will not bear close examination. His remarks on an "inverted" aedeagus presumably refer to the anteriorly directed rest position assumed by the aedeagus in certain groups of Schizophora (Nothyboidea and Muscoidea in the sense of this work). Most members of these groups are able to swing the aedeagus through a wide arc against the aedeagal apodeme by muscular action. During copulation the aedeagus is swung out, so that it becomes directed posteriorly or posteroventrally. It is clearly this copulatory position which is comparable with the position of the aedeagus in other groups of Diptera. In those groups of Schizophora in which this swinging mechanism has not evolved and the aedeagus retains a more or less fixed orientation (Lonchaeoidea, Lauxanioidea and Drosophiloidea), it is directed posteriorly or posteroventrally. The evolutionary changes which have occurred thus involve the orientation of the aedeagus, and the anus has not moved.

Munro (1947) also published criticisms of Hardy's paper, but these were made from a standpoint different from mine above, since Munro accepted Crampton's theory.

Origin and functional significance of circumversion

Since the process of hypopygial circumversion through 360° returns the aedeagus and anus to their original positions, it is scarcely possible to explain the evolution of this process on the basis of comparison of the *hypopygium circumversum* condition directly with the normal unrotated hypo-

pygium. The only authors who have speculated on this basis are Kessel and Maggioncalda (1968: 85), who suggest that circumversion may possibly bring certain advantages through greater flexibility of the postabdomen. But such an explanation hardly seems adequate to me, as the degree of flexibility of the postabdomen is more dependent on the musculature and the extent of membranous areas than on circumversion as such. Zaka-Ur-Rab (1963) appears to have despaired of finding an explanation, since he states that torsion is an "accidental development in the phylogeny of male Diptera".

Faced with this dilemma, many authors postulated an intermediate *hypopygium inversum* stage in the evolution of the cyclorrhaphous *hypopygium circumversum*. This suggestion was soundly based, since it is difficult to believe that such a major organizational change as circumversion could have been achieved in one step (apart from the rotation as such, major changes in musculature are involved). Unfortunately, confusion arose because the *hypopygium inversum* condition has evolved independently in different groups of Diptera, including many families of "Nematocera" and a few genera of "lower Brachycera" (included in the Asilidae and Bombyliidae). None of these *hypopygium inversum* conditions can be ascribed to synapomorphy with ancestors of the Cyclorrhapha, since most members of the Orthogenya, the group most closely related to the Cyclorrhapha, show a normal unrotated hypopygium. So do the great majority of other "lower Brachycera". Thus there is no group showing the *hypopygium inversum* condition which has yet been demonstrated as synapomorphous in this respect with any ancestor of the Cyclorrhapha. Kessel and Maggioncalda's (1968) suggestion that the empidid genus *Microphorus* may represent such a group requires much more investigation (see section 4). Nevertheless, the hypothesis

that there was a *hypopygium inversum* stage in the phylogeny of the Cyclorrhapha is practically inevitable in view of the recent discovery that Platypezidae copulate with the male hypopygium in the inverse position.

I set out below what seems to me the simplest possible evolutionary sequence for the evolution of the *hypopygium circumversum* condition.

1. Hypopygium normal, not rotated.
- [2. Hypopygium rotated through 180° to the inverse position during copulation (rotation reversible).]
- [3. Hypopygium rotated to the inverse position after emergence; copulation in the inverse position (rotation irreversible).]
- [4. Hypopygium rotated to the inverse position within the puparium; copulation in the inverse position (rotation irreversible).]
5. Hypopygium rotated to the inverse position within the puparium; then rotated through a further 180° to the circumverse rest position after emergence, but unwound to the inverse position during copulation (rotation partly reversible).
6. Hypopygium rotated through the full 360° to the circumverse position within the puparium; copulation in the circumverse position (rotation irreversible).

Stage 1 in the above sequence is the condition inferred for the groundplan of the Eremoneura, as retained by the Orthogenya. Stages 2, 3, and 4 (in square brackets) are still hypothetical as far as the ancestry of the Cyclorrhapha is concerned (although conditions equivalent to stages 2 and 3 are known in some groups of Diptera, as previously discussed). Stage 5 is the condition shown by all Platypezidae which have been studied. Stage 6 is the condition shown by the Schizophora and probably also by the Syrphidea. It will be seen from the above sequence that acceleration of

the process of rotation in relation to the ontogeny of the insect must be assumed to have occurred in at least two stages. The *hypopygium inversum* condition is assumed to have been reversible when first evolved, as has now been demonstrated for the *hypopygium circumversum*.

The evolution of the *hypopygium inversum* condition must clearly have been linked with a change of mating position. The platypezids which have been studied mate on the wing in an opposed (tail-to-tail) position (Kessel 1968). It is evident from the condition of reversible circumversion shown by these platypezids that the circumverse position was first evolved not as a mating position but as a rest position, which allows the external genitalia to be folded under the abdomen and thereby protected. Later the process became irreversible, and the male vertical (or "superimposed") position adopted for copulation. This is the usual mating position of the Syrphidea and Schizophora. The opposed position with one of the partners upside-down figured by Hennig (1966b) for Conopidae can be assumed from the male vertical position without any rotation of the postabdomen.

Salzer (1968) has suggested a different sequence of mating positions leading to the evolution of the *hypopygium circumversum* condition. However he was writing before the new information on the copulation of Platypezidae became available, and this clearly necessitates revision of his views. I doubt whether he was correct in postulating steps of 90° , since in those Diptera which copulate in the air rotation always involves all-or-nothing movements of about 180° .

Circumversion, deflexion and asymmetry

It is evident from my review of the literature that many taxonomists have been thoroughly confused over the relationships between circumversion,

deflexion and asymmetry. This is hardly surprising, since such confusion was inherent in the discussion of these questions by such authors as Crampton, G. H. Hardy and Aczél. Circumversion of a segment means that the segment has been rotated through 360° about the longitudinal axis of the insect. Deflexion of a segment means that the segment has been turned downwards, and I regard the longitudinal axis also as turned downwards. Asymmetry in this context means bilateral asymmetry, that is unequal development of a structure on either side of the centre-line of the insect. These words all denote different concepts.

As has been pointed out in the previous discussion, circumversion has not been demonstrated to produce asymmetry in the development of the postabdominal sclerites. In the Platypezidae circumversion occurs in two stages, 180° of the rotation occurring between the sclerites of the 7th and 8th segments, and the additional 180° between the sclerites of the 8th segment and the hypopygium. Rotation through any angle other than 180° or a multiple thereof would produce bilateral asymmetry of an originally symmetrical structure, but rotation through 180° does not. There is no convincing evidence that the asymmetry of the sclerites of the 6th and 7th segments in some groups of Cyclorrhapha is caused by anything other than asymmetrical development *in situ*. The Cyclorrhapha include many groups with a fully or nearly symmetrical postabdomen (not only the Platypezidae, but also some groups of Schizophora, such as the Drosophiloidea), and these are just as much "*hypopygium circumversum*" forms as those with a strongly asymmetrical postabdomen.

In the case of the Cyclorrhapha there seems to be a consistent correlation between circumversion and deflexion. Kessel's observations on the Platypezidae indicate that the hypopygium "passes downward" as the final

180° of rotation is completed. Deflexion and the completion of circumversion seem to be manifestations of a single process in this case. Nevertheless, we should recognize a conceptual difference between deflexion and circumversion. We would still describe a rotational movement of 360° as circumversion, even if no deflexion occurred. And there are many insects with deflexed terminalia which are not rotated. What has been observed in the Platypezidae is a complex movement which we analyse into two components, a rotational component and deflexion. Failure to appreciate the conceptual difference between rotation and deflexion has led to some confusion in the literature on Syrphidae, which I illustrate from the work of Zumpt and Heinz (1949). Zumpt and Heinz state that in *Eristalis* "we are dealing with a *hypopygium inversum*", thus apparently contradicting the view (which I hold to be correct) that all Cyclorrhapha possess a *hypopygium circumversum*. However, if Zumpt and Heinz's arguments are followed closely, it will become apparent that they have confused rotational movement and deflexion. The hypopygium of *Eristalis* is "inverse" in the sense that it is so strongly deflexed that it points anteriorly and its "dorsal" side has become ventral. But the phrase "*hypopygium inversum*" was proposed by Feuerborn (1922) for rotational inversion, as shown by some Psychodidae, Dixidae, Tipulidae and Culicidae, and does not refer to deflexion. *Eristalis* does not have a "*hypopygium inversum*" in Feuerborn's sense, but a "*hypopygium circumversum*". To prevent misunderstanding some word other than inversion should be used to describe the strongly deflexed position of the hypopygium in Syrphidae. Steyskal's (1957a) word "reflexion" seems appropriate. The hypopygium of Syrphidae may thus be described as reflexed or, if we wish to extend Feuerborn's Latin terminology, as a "*hypopygium circumversum et reflexum*".

Steyskal (1957a) rightly points out the distinction between circumversion and reflexion. But I do not understand his reference to a "third type of movement, which we may call *strophe*". In my opinion the structure of the postabdomen of all male Cyclorrhapha can be explained as the result of a combined rotational and deflexional movement followed by asymmetrical development of some sclerites *in situ* in certain groups; I see no need to postulate a third type of movement.

4. The relationship of the Cyclorrhapha to other Eremoneura

The following three sections (4 - 6) deal with classification. A summary of the classification proposed is given in table 2.

I have not undertaken a new investigation of the relationship of the Cyclorrhapha to other Eremoneura, but include this brief review of the available information as orientation for my treatment of the Cyclorrhapha. I use the names Eremoneura Lameere (1906) and Orthogenya Brauer (1883) in preference to Hennig's names Muscomorpha and Empidiformia, both on grounds of priority and because at least the use of the suffix "-morpha" leads to formal difficulties, as it is also used to indicate groups of higher rank in the classification (such as Culicomorpha and Bibionomorpha). In general the use of neutral names without connotations about rank does not seem objectionable for taxa above superfamily, and may be positively advantageous because revisions of the rank of taxa do not necessitate consequent names changes (see further the discussion by Hennig 1968b).

Characterization of the Eremoneura

The characterization of the Eremoneura (= Muscomorpha Hennig) was discussed by Hennig (1952a, 1954), who classified the Cyclorrhapha and Orthogenya (= Empidiformia) in this group. This classification agrees exactly with that proposed by Lameere (1906). Hennig referred to the following groundplan conditions which are apomorphous with respect to the groundplan of the Brachycera, as indicating that the Eremoneura probably represent a monophyletic group:

- (1) Hypopharyngeal skeleton of larvae V-shaped.
- (2) Media with only 3 branches (m_4 fused with m_3).
- (3) Anal cell closed apically; veins cu_{1b} and $1a$ with common

Table 2. Check-list of revised family classification of the Cyclorrhapha.

The names of the groups accepted in this work are listed below, to serve as a summary of the classification. All names with the suffix -idae refer to groups with the rank of family. The categories to which other groups are referred are stated. The sequence of categories used follows von K  ler (1963: 635-636), but with substitution of the name prefamily for "suprafamilia" (see section 6.1).

The list is complete for the phalanx Cyclorrhapha. The unresolved question of how other Eremoneura should be classified is discussed in section 4. The relationships of the Eremoneura to other Brachycera also require clarification. The sister-group of the Brachycera is either the whole or part of the Bibionomorpha in the sense of Hennig (1968b).

The new family names given in this list will be formally validated when the longer version of this work (which includes family descriptions) is published.

Infraorder Brachycera

Superphalanx Eremoneura (= Muscomorpha)

Phalanx Cyclorrhapha

Subphalanx Acroptera (= Anatria, Anatriata)

Lonchopteridae

Subphalanx Atriata

Infraphalanx Hypocera (= Phoridae)

Ironomyiidae

Sciadoceridae

Phoridae (inc. Termitoxeniidae)

(Cont'd)

Table 2 (Cont'd)

Infraphalanx Platypezidea

Platypezidae

Infraphalanx Syrphidea

Pipunculidae

Syrphidae

Infraphalanx Schizophora

Superfamily Lonchaeoidea

Lonchaeidae

Cryptochetidae

Superfamily Lauxanioidea

Prefamily Lauxanioinea, Lauxaniidae (incl. Celyphidae)

Prefamily Chamaemyioinea

Eurychoromyiidae

Chamaemyiidae

Superfamily Drosophiloidea

Drosophilidae

Camillidae

Curtonotidae

Campichoetidae new familyEphydriidae (incl. *Diastata*)

Superfamily Nothyboidea

Nothybidae

Teratomyzidae

Periscelididae (incl. Somatiidae)

Psilidae (= Loxoceridae)

(Cont'd)

Table 2 (Cont'd)

Superfamily Muscoidea

Prefamily Tanypezoinea

Tanypezidae (incl. Strongylophthalmyiidae)

Heteromyzidae

Prefamily Calyptratae (= Thecostomata)

Scatophagidae (= Cordiluridae)

Anthomyiidae

Fanniidae

Muscidae

Tachinidae (incl. Oestridae, Hypodermatidae, Cuterebridae, Gasterophilidae, Calliphoridae and Sarcophagidae)

Hippoboscidae family-group

Glossinidae

Hippoboscidae (incl. Nycteribiidae and Streblidae)

Prefamily Micropezoinea

Cypselosomatidae (incl. Pseudopomyzidae)

Micropezidae family-group

Neriidae

Micropezidae (incl. Calobatidae and Taeniapteridae)

Prefamily Australimyzoinea, Australimyzidae new family

Prefamily Diopsioinea

Diopsidae

Syringogastridae

Prefamily Sciomyzoinea

Coelopidae

Phaeomyiidae new status

(Cont'd)

Table 2 (Cont'd)

Dryomyzidae (incl. Helcomyzidae)

Sciomyzidae

Helosciomyzidae new status

Sepsidae family-group

Ropalomeridae

Sepsidae

Megamerinidae

Cremifaniidae new status

Prefamily Anthomyzoinea

Heleomyzidae

Rhinotoridae

Anthomyzidae

Borboropsidae new family

Trixoscelididae

Asteiidae

Opomyzidae

Sphaeroceridae (= Borboridae)

Chyromyidae

Aulacigastridae

Prefamily Agromyzoinea

Clusiidae

Agromyzidae

Prefamily Tephritoinea

Chiropteromyzidae

Mormotomyiidae

(Cont'd)

Table 2 (Cont'd)

Cnemospathidae
Odiniidae
Tethinidae
Chloropidae family-group
Acartophthalmidae
Carnidae
Milichiidae
Chloropidae (incl. Mindidae)
Conopidae (incl. Stylogastridae)
Tephritidae family-group
Eurygnathomyiidae <u>new status</u>
Richardiidae
Piophilidae (incl. Thyreophoridae and Neottiophilidae)
Tephritidae (= Trypetidae; incl. Platystomatidae, Pyrgotidae, Tachiniscidae, Otitidae, Ulidiidae, Pterocallidae and <i>Palloptera</i>)
Schizophora incertae sedis
Canacidae
Fergusoninidae
Notomyzidae <u>new family</u>
Braulidae

terminal section (the "anal vein").

In the light of my reinterpretation of Bährmann's (1960) data on the male genitalia of Empididae and my own data on the genitalia of Cyclorrhapha, I am able to add the following, all of which appear to be autapomorphous groundplan conditions of the Eremoneura:

- (4) Basimeres (♂) expanded dorsally, forming large lateral plates which are only narrowly separated on dorsum of genital segment.

This characterization depends on the validity of the periandrium hypothesis discussed in section 3.1. I postulate that the possession of separated basimeres, as in the Empidinae, is a more plesiomorphous condition than the possession of a periandrium formed by fusion of the basimeres across the dorsum of the genital segment.

- (5) Epandrium (♂) either lost or fused with cerci.

Bährmann's (1960) statement that the simplest form of epandrium in the Empididae consists of two large lobes which are fused basally on the dorsum and extend laterally towards the ventral surface of the hypopygium, refers to the type of sclerite which I call a periandrium. In those Empididae in which the basimeres remain separate (Hemerodromiinae, *Empis*, *Hilara*, *Rhamphomyia*), Bährmann reports that the epandrium is usually cleft, and that the cerci are either absent or more or less fused with the epandrium. Since a discrete epandrium and cerci are apparently never present in these insects, I suggest an alternative explanation; that the true epandrium (9th tergum) has been lost in all Eremoneura, and that the sclerites in question are all referable to the proctiger, representing modified cerci and/or 10th tergum. The presence of the 10th tergum in the groundplan of the Brachycera is indicated by the presence of this sclerite in male Rhagionidae (fig. 5).

- (6) Aedeagus (♂) slender, upcurved distally.

Bährmann (1960) did not give a precise estimate of what he thought might be the groundplan condition of the aedeagus for Empididae, beyond the general statement that "der Aedoeagus besitzt eine schlauchförmige Gestalt von unterschiedlicher Länge und ist mitunter stark gebogen". A rather slender, upcurved aedeagus was probably present in the groundplan of the Cyclorrhapha, as shown for instance by many Platypezidae and Lonchaeoidea (figs. 9, 21 and 23). The aedeagus of the Dolichopodidae and some groups of Empididae (such as *Empis* and *Rhamphomyia*) is also of this type. From this distribution I infer that a slender upcurved aedeagus was present in the groundplan of the Eremoneura. I list this condition of the aedeagus as an autapomorphous groundplan condition of the Eremoneura, since as far as I am aware such a condition is not shown in the groundplan

of other groups of Brachycera. However the information available is not complete.

The Eremoneura, as defined above, do not include *Hilaromorpha*, which Bährmann (1960) has transferred from the Empididae to the Bombyliidae. The structure of the male genitalia of *Hilaromorpha* figured by Bährmann fully supports his exclusion of this genus from the Empididae. *Hilaromorpha* shows a true epandrium in dorsal position (as in the Bombyliidae and others).

As far as I am aware, the only family of Brachycera outside the Eremoneura in which no true epandrium seems to be present is the Scenopinidae. The figures in Kelsey's (1969) revision of this family indicate that the so-called epandrium consists of a pair of lateral plates which are contiguous or slightly separated on the dorsum of the genital segment. It is possible that these plates represent laterally situated basimeres (as in the groundplan of the Eremoneura), rather than a cleft epandrium. However, the larvae of the Scenopinidae do not show the modifications characteristic of the Eremoneura, but are very similar to the larvae of the Therevidae (Hennig 1952a). If the Scenopinidae are in fact more closely related to the Therevidae than to the Eremoneura (as is currently believed), then the similarity between the genitalia of the Scenopinidae and Eremoneura can only be ascribed to convergence or parallelism. On the other hand, if the similarities between the Therevidae and Scenopinidae are due to symplesiomorphy, the possibility that the Scenopinidae are the sister-group of the Eremoneura cannot be excluded. I offer no opinion on this question, but draw attention to it for consideration in future studies.

Protempididae

Until recently no information on the age of the Eremoneura was available, but Ussatchov (1968) has described as *Protempis* (Protempididae) a relevant fossil species from Jurassic deposits in Kazakhstan. The wing venation of *Protempis* corresponds exactly with what can be inferred about the groundplan condition of the wing venation for Eremoneura. The Protempididae may thus represent the stem-group of the Eremoneura, in accordance with the definition of "stem-group" proposed by Hennig (1965b). The full suite of plesiomorphous conditions shown by *Protempis* is not shown in combination by any recent species, as far as I am aware, although a few recent species classified in the Empididae have wing venation little removed from that of *Protempis*.

Characterization of the Cyclorrhapha

The Cyclorrhapha (= Musciformia Hennig) are a subordinate monophyletic group of the Eremoneura. The earliest known fossil Cyclorrhapha are from the Cretaceous Period (see J. F. McAlpine and Martin 1969 and J. F. McAlpine 1970). The apomorphous conditions of the Eremoneura are as follows:

- (1) Larval head capsule reduced; individual parts of cephalic and pharyngeal skeleton fused into uniform "cephalopharyngeal skeleton"; pupa enclosed within puparium formed by contraction and hardening of integument of 3rd larval instar.

The morphology of the larvae of Cyclorrhapha was reviewed by Hennig (1952a). The name Cyclorrhapha, first proposed by Brauer, refers to the circular ecdysial suture around the first abdominal segment of the larva and puparium of most Schizophora (except Cryptochetidae). However Hennig indicated that the position of the ecdysial sutures on the puparia of other groups of Cyclorrhapha varies, and the groundplan condition for the group as a whole has not been established.

- (2) Radial sector two-branched; r_{4+5} not forked (Hennig 1954).

This condition is also shown by various groups of Empididae and such reduction may in some cases represent synapomorphy with the Cyclorrhapha.

The second venational character given by Hennig (1954), loss of r_3 , does not in my opinion differentiate the groundplan of the Cyclorrhapha from the groundplan of the Eremoneura, since the presence of an apparent r_3 as a cross-vein in *Dolichocephala* (Empididae) is most probably secondary (apomorphous). Such a vein is not normally present in other Brachycera except in members of groups which show a clear tendency to develop additional cross-veins (in particular the Nemestrinidae and some Bombyliidae).

- (3) Hypopygium (♂) rotated to inverse position within puparium, then rotated through further 180° to circumverse rest position soon after emergence; 8th abdominal segment rotated through half angle of hypopygial rotation (through 90° within the puparium, then through further 90° to inverse position after emergence).

This characterization is the result of the analysis presented in section 3.2. The postulated groundplan condition is retained by the Platypiezidae.

- (4) 8th tergum (♂) (normally in ventral position in mature adult) reduced to narrow band (fig. 10).

Reduction of the 8th tergum also occurs in *Atelestus* and in some other genera of Empididae (see Bährmann 1960, fig. 1). Since the Empididae are probably paraphyletic (see below), the possibility that such reduction may represent synapomorphy with the Cyclorrhapha should be borne in mind. The reduced 8th tergum in these Empididae is dorsal, since their postabdomen is not rotated.

Atelestus

The delimitation of the Cyclorrhapha has long been largely settled, and the only remaining dispute in recent literature concerns the classification of the genus *Atelestus* (= *Platynema*). Most authors have included this genus in the Empididae, but others (notably Kessel 1960 and Krystoph 1961) have referred it to the cyclorrhaphous family Platypiezidae. Clearly there is substance in the arguments of Kessel and Krystoph that *Atelestus* is strongly divergent from most other Empididae and shows certain resemblances to the Platypiezidae. Another resemblance, besides those stated by these

authors, is in the structure of the male genital segment (figs. 6 and 7). This bears a large symmetrical periandrium, agreeing remarkably with the condition shown by the Cyclorrhapha. Nevertheless, I do not think that *Atelestus* should be included in the Platypezidae, because it shows at least one feature which seems to me irreconcilable with such a classification: this is that the 8th abdominal segment of the male bears a narrow band-like sclerite dorsally and a large sclerite ventrally. This is the reverse of the groundplan condition for the Cyclorrhapha (retained by the Platypezidae), in which the inverted 8th segment bears its large sternum in a dorsal position. The obvious inference from the condition of the 8th segment shown by *Atelestus* is that its terminalia are not rotated: at any rate it seems reasonable to assume this unless contrary evidence can be found, for instance from dissection of fresh material (which was not available to me). If *Atelestus* does not possess rotated terminalia, then the genus cannot be referred to the Platypezidae (or any other cyclorrhaphous family), and the possibility must be considered that its resemblances to the Platypezidae are in fact resemblances to the groundplan of the Cyclorrhapha as a whole. Since the Platypezidae show the least modified adult morphology of all groups of Cyclorrhapha in many respects, such an interpretation raises no conceptual difficulty. The question of how *Atelestus* should be classified probably cannot be settled at present, since the phylogenetic relationships of the groups currently included in the Empididae require clarification. Pending such clarification I think it best to retain the conventional classification of the genus in the Empididae for purposes of nomenclature.

The Orthogenya

Brauer (1883) proposed the group Orthogenya to include the Empididae

and Dolichopodidae, that is all Eremoneura excluded from the Cyclorrhapha. Identical group concepts were also proposed by Lameere (1906) ("Orthorrhapha") and Hennig (1952a, 1954) ("Empidiiformia"). Hennig's discussions of this group have been concerned mainly with demonstrating its affinity with the Cyclorrhapha. The question of whether the Orthogenya are monophyletic or paraphyletic (containing more than one lineage of non-cyclorrhaphous Eremoneura), has not been settled. Aczél (1954) and Kessel and Maggioncalda (1968) have implied that the Orthogenya are not monophyletic, because they suggest that particular groups of Orthogenya are more closely related to the Cyclorrhapha. I do not think that this question can be settled from existing analyses, but briefly review these authors' views with the aim of clarifying the issues involved.

Aczél (1954) considered that the Dolichopodidae should be grouped with the Cyclorrhapha, and consequently proposed a new subdivision of the Brachycera into two "Divisions", the Orthopyga and Campylopyga. He included in the Campylopyga the Dolichopodidae and Cyclorrhapha, and characterized the group as follows:

"Male postabdomen without exception folded beneath last tergite of the preabdomen and circumverted. Antennae inserted below the prefrontal suture and consisting of three segments, scape, pedicel and postpedicel only."

The value of the form of the antennae in indicating the relationships of the Dolichopodidae is uncertain, since there is no clear-cut distinction between the types of antennae shown by the Cyclorrhapha, Dolichopodidae and some groups of Empididae. Further investigation of the character sequence involved is needed. The part of Aczél's characterization which I am able to assess definitively is the first sentence, which implies that the Dolichopodidae possess a *hypopygium circumversum* and are hence

monophyletic with the Cyclorrhapha. Until recently some doubt has remained as to whether this is correct. Hardy (1953) stated that in Dolichopodidae the alimentary and genital tracts are "in one plane", and that "this difference in anatomical detail shows that the Dolichopodidae are not in the direct evolutionary line that leads to Cyclorrhapha". However D. K. McAlpine (1960) stated that "in *Sciapus* the relative twisting of the hind gut and vas deferens is indicative of circumversion". Bährmann (1966) has clarified these apparent contradictions. He reports that the genus *Dolichopus* contains species without looping of the ejaculatory duct over the hind gut, as well as species in which such looping is almost complete. He concludes that the irregularity of this looping is evidence against the assumption of synapomorphy between the Dolichopodidae and Cyclorrhapha in respect of hypopygial rotation. Thus the only demonstrated similarity between the hypopygia of the Dolichopodidae and Cyclorrhapha is that in both groups the hypopygium is deflexed. This does not provide sufficient grounds for inferring that the Dolichopodidae are monophyletic with the Cyclorrhapha, when the detailed structure of the hypopygium is very different in the two groups. The hypopygium in the Dolichopodidae is enclosed by a highly modified "genital capsule", which is connected with the preceding segment only through a narrow opening situated asymmetrically on its left side (Bährmann 1966). This capsule is more or less uniformly sclerotized, and its homology is in doubt. However, its muscular connections with the aedeagal apodeme suggest that it is largely of hypandrial origin (see Bährmann 1966: 70). Possibly the nearest relatives of the Dolichopodidae should be sought amongst those groups referred to the Empididae in which the hypandrium is enlarged at the expense of the basimeres (as for instance in *Heleodromia*). Bährmann (1960) discusses

the possibility of such a relationship, but reaches no definite conclusion. Thus, although the available analyses of the relationships of the Dolichopodidae are not conclusive, it seems unlikely that Aczél's *Campylopyga* is monophyletic, and I therefore follow Hennig, Bährmann and others in rejecting Aczél's classificatory proposals.

Kessel and Maggioncalda (1968) have advanced a different hypothesis about the relationship of the Cyclorrhapha with particular groups of Empididae, in elaboration of views expressed by Kessel in earlier papers. These authors consider that the Cyclorrhapha are phylogenetically related to certain genera of Empididae ("that branch of the Hybotinae which leads to the Platypezidae"). The genera stated to belong to this "branch" are *Meghyperus*, *Ocydromia*, *Leptopeza*, *Bicellaria*, *Euthyneura*, *Oedalea*, *Syndyas*, *Trichina*, *Hybos* and *Microphorus*. The order in which the authors comment on these genera (as given in my previous sentence) corresponds with the degree of apparent rotation of the postabdomen. *Meghyperus*, whose hypopygium is fully symmetrical, is considered as "the perfect representative of the ancestral line forming the base of that branch of the Hybotinae which leads to the Platypezidae"; *Ocydromia* and *Leptopeza* are then mentioned as "other primitive genera". The authors then mention *Bicellaria*, *Euthyneura*, and *Oedalea* as examples of genera "in which there is already a slight twist of the postabdomen towards the right. At still a higher level, and in such genera as *Syndyas*, *Trichina* and *Hybos*, this twist has become a full 90-degree rotation with reference to the main axis of the abdomen, and this rotation has become the rule in that hybotine line which leads towards Platypezidae and Tachydromiinae". Finally, *Microphorus* is discussed, "a genus of Hybotinae above *Hybos* and also representing the empidid stock leading to Platypezidae. In this form the postabdomen is stalked and bears the

hypopygium in inverted position, the relationships of these male sexual structures resembling those of Platypezidae at the time of emergence". These statements imply that the Orthogenya are not monophyletic, since a particular group of Empididae is considered to be "ancestral to the platypezids". The latter phrase should not, however, be taken as a denial of the monophyly of the Cyclorrhapha, since the authors explicitly state (page 103) that they are convinced that the Cyclorrhapha are properly considered to be a monophyletic group.

Kessel and Maggioncalda's argument is mainly based on placing conditions of the hypopygium shown by Recent forms in a series which they believe to represent stages in the evolution of the cyclorrhaphous hypopygium. In attempting to judge to what extent their conclusions are warranted, I now consider their argument in the light of the two recent comparative morphological studies of the Empididae by Bährmann (1960) and Krystoph (1961).

I must first remark that the Hybotinae in the sense followed by Kessel and Maggioncalda are no doubt paraphyletic. Both Bährmann and Krystoph use the name Hybotinae in a more restricted sense, and conclude that the Hybotinae (in their restricted sense), the Ocydromiinae and the Tachydromiinae together form a monophyletic group. This group is well characterized by apomorphous conditions of the mouthparts (Krystoph 1961). The tormae are free from the clypeus in their lower two-thirds, not articulated with the labrum, but standing separate from it on the margins of the cibarium; the maxillary laciniae have been lost, and the palpi are separated from the maxillae (borne on palpifers).

Of the genera stated by Kessel and Maggioncalda to belong to their "branch leading to the Platypezidae", all belong to the Hybotinae/Ocydromiinae/

Tachydromiinae group of Krystoph, with the exception of the last genus *Microphorus* (discussed further below). However, the markedly apomorphic features of the mouthparts shown by this group clearly exclude the possibility that the Cyclorrhapha were derived from it (in the sense of having a more recent common ancestry with particular genera within the group than these have with each other). In many Cyclorrhapha well-developed maxillary laciniae are retained, and a palpifer of the type stated is not developed; the tormae are usually not separated from the labrum in the manner stated. Such conditions are plesiomorphous in comparison with the conditions shown by the Hybotinae/Ocydromiinae/Tachydromiinae group, and indicate that the Cyclorrhapha could not have been derived from this group, although the possibility of some close relationships between the Cyclorrhapha and the group as a whole is not thereby excluded. The "rotated" hypopygia shown by certain genera within this group cannot be ascribed to synapomorphy with conditions shown by ancestors of the Cyclorrhapha. In many genera of the group the hypopygium seems unrotated; and apparent rotation, where it occurs, is usually associated with asymmetrical modifications of the perianthrium (which is almost invariably symmetrical in Cyclorrhapha). I am doubtful whether any true rotation in fact occurs, since the change in the orientation of the genitalia may be the result of asymmetrical development *in situ*. I think that the sequence of hypopygial modifications shown by members of the Hybotinae/Ocydromiinae/Tachydromiinae group proceeded independently of the evolution of the *hypopygium circumversum* condition of the Cyclorrhapha. If there was a common ancestor of the Cyclorrhapha and that group, this probably had a symmetrical unrotated hypopygium, as in *Atelestus* (figs. 6 and 7).

The genus *Microphorus* is probably related to the Hybotinae/Ocydromiinae/

Tachydromiinae group according to Krystoph (1961), but retains a more plesiomorphous maxilla; the laciniae are well developed and the palpi in normal position, borne on the maxillae (without any intervening palpifer). Similar plesiomorphous conditions must be assumed for ancestors of the Cyclorrhapha (but are not evidence of phyletic relationship, which can only be inferred from common possession of apomorphous conditions). The common apomorphous condition of the mouthparts which led Krystoph to infer a relationship between *Microphorus* and the Hybotinae/Ocydromiinae/Tachydromiinae group, is the structure of the tormae. The condition of the tormae in the groundplan of the Cyclorrhapha is thus highly relevant to the suggestion of an affinity between the Cyclorrhapha and *Microphorus*, but I am not at present able to judge this question. Frey's (1921) classical comparative study of the mouthparts was unfortunately confined to the Schizophora; there is insufficient comparative information on the mouthparts of the other subgroups of the Cyclorrhapha. It certainly seems possible that the condition of the postabdomen shown by *Microphorus* represents (through synapomorphy) a stage in the evolution of the conditions shown by the Cyclorrhapha, since the inverted position and rightward direction of the 8th segment and the hypopygium in this genus resembles the condition shown by newly emerged platypezid males (as Kessel and Maggioncalda have stated). But further detailed comparative studies are needed before firm conclusions can be drawn.

The conclusion which I draw from the above discussion is that, while there are good reasons for doubting whether the Orthogenya are monophyletic, the authors who have raised this question have not made sufficiently extensive studies to settle the matter.

The views of Hennig (1970)

Shortly before completing the manuscript of this work I received a new paper by Hennig (1970), in which he reviews some of the material which I have covered (independently) in the preceding discussion. Hennig also affirms that the Hybotinae/Ocydromiinae/Tachydromiinae group is monophyletic, and discusses other characters in addition to those which I have mentioned. He suggests that this group can probably be classified with the Microphorinae and Atelestinae in a "subfamily-group" Ocydromioinea, while all other Empididae can be referred to another group of the same rank, the Empidoinea.*

This seems a useful working classification for the present, although doubt must remain about whether these "subfamily-groups" are monophyletic until the relationships of the Dolichopodidae and Cyclorrhapha have been clarified. The groups which Hennig includes in the Ocydromioinea are those which show a periandrium, and I think that the possibility that the whole or part of this group is more closely related to the Cyclorrhapha than to other "Empididae" remains open (see previous discussion).

In this paper Hennig expresses doubt about the monophyly of the Eremoneura on the basis of a character not previously considered, the structure of the antennal arista. He points out that a three-articled arista (with two small basal articles) must be ascribed to the groundplan of the Cyclorrhapha, but the arista has only two articles in those recent Orthogenya which he examined (including *Atelestus*). This character seems to him to indicate the possibility that the Orthogenya should be included

*Hennig's use of the suffix "-oinea" for "subfamily-groups" is inconsistent with the proposal of von K  ler (1963) to use this suffix for a category between family and superfamily (see section 6.1). But this discrepancy is likely to be removed in future revisions, since the present wide limits of the "Empididae" are untenable.

in the Asilomorpha (which have a two-articled arista), as in Rohdendorf's (1964) classification, rather than considered more closely related to the Cyclorrhapha.

I do not share Hennig's doubts about the monophyly of the Eremoneura, and think he is placing too much weight on one character in isolation. The evidence for the monophyly of the Eremoneura has become very substantial. To the resemblances in wing venation and larval morphology discussed in Hennig's previous works, I can now add the similar structure of the male genital segment. In particular, the genus *Atelestus* shows certain strong similarities to some groups of Cyclorrhapha (such as the Platypezidae), which cannot be summarily dismissed as due to convergence. The hypothesis that the similarities between *Atelestus* and the Platypezidae are retained from a common ancestor of the Ocydromioinea and Cyclorrhapha has much to commend it. If Hennig's suggestion that the Cyclorrhapha may be the sister-group of the Asilomorpha (including Orthogenya) is correct, then we must infer the existence of an independent lineage leading to the Cyclorrhapha at least since the Jurassic Period. Any fossils belonging to this lineage would be recognizable by a series of antennal modifications leading to the formation of a three-articled arista. But nothing in the assemblages of Jurassic Diptera so far described suggests the existence of such an independent lineage. In default of such contrary evidence, I think that the three-articled arista condition was probably derived from the two-articled condition, not through an independent series of modifications. This interpretation is fully compatible with the evidence of other characters.

5. The major subordinate groups of the Cyclorrhapha

The characterization of the Cyclorrhapha has been discussed in the previous section. Hennig (1952a) followed de Meijere (1900) in dividing the Cyclorrhapha into two sister-groups: the Acroptera (= Anatriata) containing the single family Lonchopteridae, and the Atriata containing all other Cyclorrhapha (fig. 13). I also accept this division, but prefer to use Brauer's (1883) name Acroptera to Hennig's Anatriata (= Anatria de Meijere) on grounds of priority. Many authors still follow a traditional division of the Cyclorrhapha into the Aschiza and Schizophora. However only the latter group is monophyletic. The "Aschiza" constitute a residual paraphyletic assemblage of all Cyclorrhapha which are excluded from the Schizophora because they lack a ptilinum. To my knowledge it has never been claimed that the Aschiza show any apomorphous conditions in common. Such a group has no place in a phylogenetic classification in the sense followed in this work.

The justification for the division of the Cyclorrhapha into the Acroptera and Atriata rests largely on larval characters. In the Acroptera a small remnant of the larval head capsule is visible in dorsal view (de Meijere 1900, Hennig 1952a), a relatively plesiomorphous condition in comparison with the highly apomorphous "headless" condition shown by all other cyclorrhaphous larvae, in which no free remnant of the head capsule is visible externally. Adult lonchopterids are of uniform appearance, characterized by several apomorphous conditions, for instance in the shape and venation of the wing (see Hennig 1954). Thus there appears to be an alternance of apomorphous and plesiomorphous conditions between the Acroptera and Atriata, which is the basis for inferring that these groups

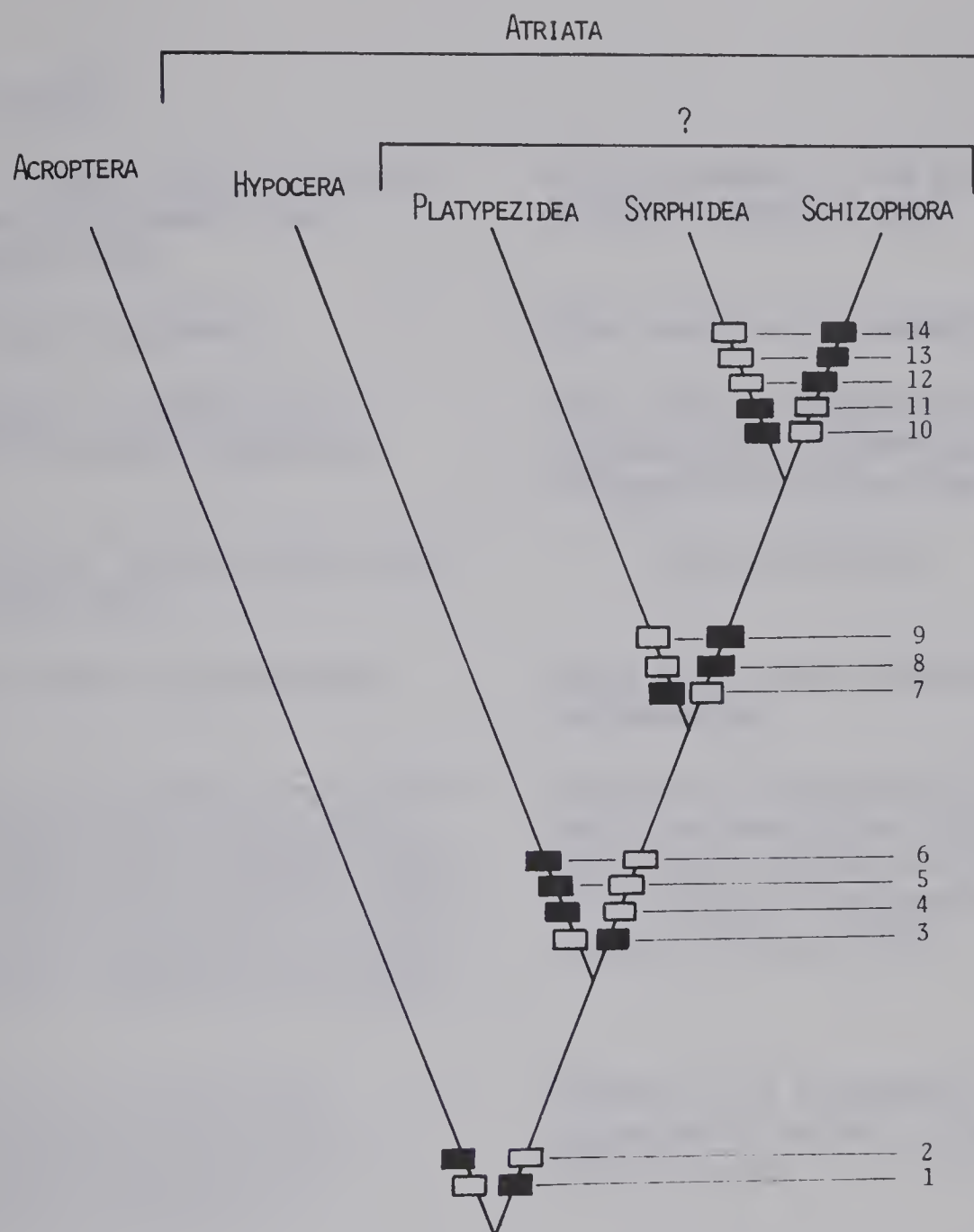


Fig. 13. Systematic division of the Cyclorrhapha, in accordance with the argumentation scheme of phylogenetic systematics.

Apomorphous conditions
(black rectangles)

1. Larval head capsule reduced:
atrium formed
2. Shape and venation of wing
modified
3. m_1 and m_2 forked beyond discal
cell or at least at its distal
corner
4. Subcosta partly fused with r_1
5. Anal cell shortened

Plesiomorphous conditions
(white rectangles)

- Small head capsule retained:
atrium absent
- Wing as in groundplan of
Cyclorrhapha
- Distal section of m_2 arising from
discal cell
- Subcosta complete
- Anal cell elongate

(cont'd)

Fig. 13 (Cont'd)

- | | |
|--|---|
| 6. Only a single dorsal sclerite between 6th segment and hypopygium (♂) | All sclerites of 7th and 8th segments retained (♂) |
| 7. Hind tarsi expanded | Hind tarsi not expanded |
| 8. Hypopygial circumversion completed within puparium (♂) | Final 180° of hypopygial circumversion occurring after emergence from puparium (♂) |
| 9. Ejaculatory apodeme free from body wall (♂) | (not clarified) |
| 10. Frons without macrochaetae | Frons with well differentiated macrochaetae |
| 11. 6th and 7th abdominal segments asymmetrically developed on left side, with reduced terga; 8th sternum enlarged and asymmetrical; hypopygium strongly deflexed, directed anteriorly (♂) | Postabdomen symmetrical or only weakly asymmetrical; 6th and 7th terga not reduced; 8th sternum not enlarged; hypopygium less strongly deflexed (♂) |
| 12. Ptilinum and temporary musculature present: 1st abdominal segment with adventitious suture | Ptilinum and temporary musculature absent: adventitious suture absent |
| 13. m_{1+2} not forked | m_{1+2} forked |
| 14. Anal cell shortened | Anal cell elongate |

are sister-groups in the sense proposed by Hennig (1950, 1966a).

The name Atriata refers to the formation of an "atrium" before the primary mouth opening of the larva (see Hennig 1948b). The "headless" condition of the larva is clearly one of considerable complexity (in the sense in which I use this term in section 2.3), and thus provides firm grounds for inferring that the Atriata are monophyletic. The groups of Atriata which show the least modified adult morphology are the Platypezidae and Ironomyiidae. When the adult morphology of members of these families is considered, it is scarcely possible to find autapomorphous conditions of the Atriata, except perhaps for reduction of the costa on the posterior margin of the wing (given as an apomorphous condition of this group by Hennig 1954). However the difference in this respect is slight, since in *Opetia* a trace of sclerotization around the posterior margin of the wing is still apparent (Hennig 1954). In respect of all other characters so far analysed, the groundplan condition of the adult stage of the Atriata seems not to differ from the relevant groundplan condition of the Cyclorrhapha as a whole.

The structure of the Platypezidae has already been discussed in section 3.2, in the light of Kessel's recent discovery that in this group part of the hypopygial rotation in the male does not take place until after emergence from the puparium. This condition corresponds to an earlier stage in the evolution of the irreversible "*hypopygium circumversum*" condition shown by the Schizophora, in which circumversion is completed within the puparium. The segmental sclerotization of the male postabdomen of some Platypezidae, such as *Plesioclythia* (figs. 10 and 11), is the least modified of that shown by any cyclorrhaphan known to me. The 6th and 7th segments bear well developed terga and sterna in the normal dorsal

and ventral positions. The 7th sternum is more or less symmetrical, or appears slightly asymmetrical due to weaker sclerotization of its right side (as in fig. 10). The 8th segment bears a large sternum, which is dorsally situated (inverted) when the hypopygium is in its circumverted rest position; the 8th tergum is reduced to a narrow band, which in *Plesioclythia* (fig. 10) extends from the venter around the right side of the insect (in the rest position). The 8th segment is rotated through half the angle of hypopygial rotation, which results in the sternum occupying a lateral position on the left side at emergence and during copulation, when the hypopygium is inverted (rotated through only 180°). The arrangement of postabdominal sclerites shown by the Platypezidae corresponds closely with what can be inferred about the groundplan condition for the Schizophora, and the conditions shown by other groups of Atriata are derivable from such a condition. For this reason I am convinced that one of the keys to an understanding of the morphological changes which have occurred in the male postabdomen of various groups of Atriata lies in detailed study of the Platypezidae. However, another consequence of the retention of many plesiomorphous conditions by the Platypezidae is that it is difficult to interpret their relationships to other Atriata because of a paucity of apomorphous conditions, at least as known from existing analyses. Hennig (1952a, 1954) accepted the classification of this family in the Hypocera (following Brauer 1883), but was not able to advance any clear-cut apomorphous conditions to demonstrate the validity of this classification. His comment that all the families of Hypocera show a "tendency to reduction of the discal cell" (Hennig 1954: 360) is unconvincing. If the character sequence involved in the reduction of the discal cell in true Hypocera is compared with the condition shown by the Platypezidae,

the latter condition does not appear to belong to the same sequence. In *Ironomyia* (an undoubted hypoceran) the distal section of vein m_2 arises from the discal cell (J. F. McAlpine 1967, fig. 3), as in the postulated groundplan of the Eremoneura (corresponding to the conditions shown by the Jurassic Protempididae and some recent groups of Empididae). In Platypezidae the discal cell is elongate and bounded distally only by the posterior cross-vein (m-m); the fork of veins m_1 and m_2 lies beyond the discal cell, or at least at its distal corner (in *Platypezina*). This apomorphous condition of the median field of the wing is hardly different from the groundplan condition of the Syrphidea, and the condition shown by the Schizophora probably represents a further modification of the same character sequence (differing from the groundplan of the Platypezidae and Syrphidea in respect of loss of the fork of m_{1+2}). Thus the evidence of the wing venation does not support the classification of the Platypezidae in the Hypocera, but suggests that this may be incorrect. If it is later confirmed that the Platypezidae, Syrphidea and Schizophora are monophyletic, Schiner's (1864) name Orthocera is available for such a group.

J. F. McAlpine and Martin (1966) also accepted the classification of the Platypezidae in the Hypocera as a starting point for their studies. In that paper they reconstructed some aspects of the groundplan of the Hypocera ("the original phoroid fly") by comparing conditions shown by *Ironomyia* (Ironomyiidae) and the platypezid genera *Platypezina*, *Opetia*, *Microsania* and *Melanderomyia*. However, if the Platypezidae are not referable to the Hypocera, then the most recent common ancestor of the Platypezidae and Ironomyiidae may well have been the common ancestor of the Atriata as a whole, and McAlpine and Martin's characterization of the "original phoroid fly" may consequently refer to the groundplan of the Atriata. I do not

find in their data any strong support for the view that the Platypezidae are more closely related to the undoubted hypoceran families (Ironomyiidae, Sciadoceridae and Phoridae) than to the Syrphidea or Schizophora. Clearly the relationship of the Platypezidae to other Atriata is in need of further study. In table 2 I provisionally list the Platypezidae as constituting one of the major subordinate groups of the Atriata, the Platypezidea (a name already proposed by Rohdendorf 1964). This classification leaves open the question of whether the group is most closely related to the Hypocera, Syrphidea or Schizophora. A sound basis for further studies of the Platypezidae has been provided by Kessel and Maggioncalda's (1968) revision. The presence of expanded hind tarsi at least in the male (clearly an apomorphous condition) suggests that at least the majority of the genera accepted as Platypezidae by these authors constitute a monophyletic group. However *Atelestus* (= *Platycnema*) should not in my opinion be referred to this family (see section 4). Kessel and Maggioncalda have also accepted as Platypezidae two other problematical genera, *Opetia* and *Melanderomyia*, which they consider to be "primitive" Platypezidae. Both genera are unknown to me. Neither shows the tarsal modification characteristic of the other genera referred to the Platypezidae. Since none of the other diagnostic characters of the Platypezidae have yet been shown to be autapomorphous, the possibility remains that these genera may be misplaced or may represent a group or groups meriting separate family status. Detailed morphological studies on *Opetia* and *Melanderomyia* might thus advance our understanding of the evolution of the Atriata. But until further information is available, I provisionally accept the classification of these genera in the Platypezidae. The larvae of *Melanderomyia* are known to be fungivorous, as are all the known larvae of undoubted Platypezidae, but no description

is available.

As a consequence of my exclusion of the Platypezidae, I restrict the limits of the Hypocera (= Phoridae) to the Ironomyiidae, Sciadoceridae and Phoridae (including Termitoxeniinae). The characterization of this group has been clarified by Hennig (1954, 1964), J. F. McAlpine and Martin (1966) and J. F. McAlpine (1967). These studies indicate that the Hypocera are characterized in their groundplan by the following apomorphous conditions with respect to the groundplan of the Atriata:

- (1) Apex of second antennal article deeply inserted into base of third.
- (2) Subcosta partly fused with vein r_1 .
- (3) Anal cell shortened.
- (4) Male postabdomen with only one dorsal sclerite between 6th segment and hypopygium.

The groundplan condition of the wing venation in Hypocera is probably that shown by the Tasmanian *Ironomyia* (see J. F. McAlpine 1967). The structure of the male postabdomen of *Ironomyia* (McAlpine 1967, figs. 9 and 10) also appears more plesiomorphous than that of the Phoridae, in which the protandrial sclerites are still more reduced. My statement of the groundplan for the Hypocera (character 4 above) consequently refers to the condition shown by *Ironomyia*. This characterization may possibly need revision, when information becomes available on the structure of the male postabdomen of recent Sciadoceridae. The available descriptions of the latter family do not give details of the postabdomen and genitalia.

The works of Hennig (1964), J. F. McAlpine and Martin (1966) and J. F. McAlpine (1967) have considerably advanced our understanding of the evolution of the Hypocera. McAlpine and Martin's proposal of a new

family Ironomyiidae based on the Tasmanian *Ironomyia nigromaculata* White seems justified by the information presented, which suggests that this species is the sister-group of all other known Hypocera. Following these authors I recognize three families of the Hypocera in the restricted sense here followed: the Ironomyiidae, Sciadoceridae and Phoridae. McAlpine and Martin's key summarizes the characterization of these families. The Termitoxeniinae (hermaphroditic forms living in termite colonies) are a subordinate group of the Phoridae in the phylogenetic system. Rohdendorf's (1964) proposal of infraordinal rank ("Termitoxeniomorpha") for this group reflects his phenetic principle of classification in accordance with which highly divergent groups are given high rank in the system. He does not interpret the phylogenetic relationships of the group differently, for he states it to be a "very altered descendant of the Phoridae".

The third major subordinate group of the Atriata here recognized is the Syrphidea. This group is conventionally divided into two families, the Pipunculidae and Syrphidae, whose close relationship to each other has long been accepted. Hennig (1954) characterized the group on the basis of wing venation, indicating the following apomorphous conditions with respect to the groundplan of the Atriata:

(1) m_1 and m_2 arising with common stem from discal cell.

(2) m_2 not reaching wing margin.

However this characterization does not demonstrate the monophyly of the Syrphidea, since the wing venation of the Schizophora may be a further modification of the groundplan condition of the Syrphidea. Autapomorphous conditions which constitute more conclusive evidence of the monophyly of the group are as follows:

(3) Frons without conspicuous macrochaetae.

- (4) 6th and 7th abdominal segments (♂) asymmetrically developed on left side, with terga relatively small in comparison with large sterna.
- (5) 8th sternum (♂) enlarged and strongly asymmetrical, occupying terminal position on abdomen.
- (6) Hypopygium (♂) very strongly deflexed and directed more or less anteriorly, adpressed against right side of protandrium when at rest.
- (7) Ejaculatory apodeme free from body wall (♂) (fig. 8).

The structure of the male postabdomen of the Syrphidea was correctly interpreted in Metcalf's (1921) now classical paper, except that his numbering of segments requires revision. Metcalf accepted a theory then current that a segment had been lost at the base of the abdomen in Diptera. This theory now seems defunct, and consequently all Metcalf's segment numbers should be reduced by one. Unfortunately, much confusion has arisen in the literature on the Syrphidea because some subsequent workers have not accepted Metcalf's homologies, due apparently to an assumption that the larger sclerite of any segment must be the tergum. Aczél's (1948) homologies of the postabdominal sclerites of the Pipunculidae clearly illustrate the untenable consequences to which rigid adherence to this assumption can lead. Aczél stated that terga are usually more resistant to reduction than sterna in the Diptera, because the sterna of the preabdominal segments are usually smaller than the terga. Applying this principle to the structure of the male abdomen of the Pipunculidae, he counted the first six abdominal terga in the normal manner, but then numbered the 6th to 8th sterna as the "7th tergite", "8th tergite" and "epandrium" or "9th tergite". He consequently considered the true genital segment to be the 10th visible segment,

which is scarcely tenable because workers on other groups of Diptera have never reported more than eight visible segments before the genital segment. Zumpt and Heinz (1949) also confused the postabdominal terga and sterna, and their work was justifiably criticized by Hardy (1950) and van Emden (1951) on this account. Such confusion was in fact unnecessary, since Metcalf (1921) had given figures of the tracheation of the postabdomen which demonstrated that his interpretation of the terga and sterna of the 6th and 7th segments was correct. The large sclerite of the 8th segment (called "urite nine" by Metcalf because he was not sure whether it was a tergum or a sternum) should clearly be homologized with the inverted 8th sternum on the basis of comparison with the structure of other Cyclorrhapha. Metcalf did not mention any sclerite which might represent the 8th tergum, but I have noted a small sclerotized band which possibly represents a remnant of this sclerite in *Xylota* (Syrphidae). In respect of the condition of the ejaculatory apodeme the Syrphidea are probably synapomorphous with the Schizophora (see the discussion in section 3.1).

The fourth major subordinate group of the Atriata is the Schizophora, which are treated in detail in the next section of this work. The Schizophora are characterized primarily by the development of a new and complex organ, the ptilinum, associated with temporary musculature in the first four abdominal segments. The temporary muscles pump haemolymph into the ptilinum; after retraction of the ptilinum the temporary abdominal muscles, as well as the muscles of the ptilinum itself, are broken down. This complex condition involves such major structural and physiological modifications that it is scarcely possible to doubt that the Schizophora are monophyletic. Strickland (1953) has published a comparative study of the structure of the ptilinum. The name Schizophora (proposed by Becher 1882)

refers to the ptilinal suture which remains on the frons and face of the mature fly as a result of retraction of the ptilinum. Additional apomorphous groundplan conditions of the Schizophora with respect to the groundplan of the Atriata are as follows:

(2) Vein m_{1+2} not forked.

(3) Anal cell shortened.

In some members of a few schizophorous families, notably the Conopidae and Micropezidae, the anal cell is elongate, reaching to near the wing margin. But Hennig (1958) concluded that the elongate anal cell has probably evolved secondarily in these groups, with uncertainty remaining only in respect of the Conopidae. However, if my reference of the Conopidae to the Tephritoinea is accepted (see section 6.2), then the elongate anal cell shown by some members of this family must also be interpreted as secondary.

(4) Two pairs of vertical bristles (*vti* and *vte*) present.

Most Schizophora are characterized by well differentiated frontal and vertical bristles, including typically 1-3 orbital bristles, a pair of anteriorly directed ocellar bristles, two pairs of vertical bristles (of which the *vti* are directed inwards and the *vte* outwards) and a pair of postvertical bristles. Some of these may be homologous with bristles shown by other Cyclorrhapha, such as the Platypezidae and Hypocera; but at least the presence of two pairs of vertical bristles can be considered an autapomorphous condition of the Schizophora, since no more than a single pair are shown by other cyclorrhaphans. Whether the presence of well differentiated postvertical bristles is also an autapomorphous groundplan condition of the Schizophora is not clear, as these bristles are scarcely differentiated in members of the Lonchaeoidea. Hennig (1958) has discussed the chaetotaxy of the head in the Schizophora in some detail.

(5) Hypopygium (♂) irreversibly rotated through 360° to circumverse position within puparium.

I have reviewed the subject of hypopygial rotation in section 3.2. There I concluded that the completion of circumversion within the puparium is a more apomorphous condition than the condition shown by the Platypezidae, in which the last 180° of rotation is facultative and occurs only after emergence from the puparium. Unfortunately, detailed observations on the process of circumversion in the Syrphidea and Hypocera are not yet available, so that it is not clear whether these groups are synapomorphous with the Schizophora in respect of this character.

(6) First abdominal segment with "adventitious suture" extending posterodorsally from its anterior margin (Young 1921).

I suspect that the adventitious suture is a ridge serving as attachment

for some of the temporary muscles which pump haemolymph into the ptilinum. But I have not been able to find any definite information on this point.

(7) Ejaculatory apodeme (♂) free from body wall.

See the discussion in section 3.1. The same condition is shown by the Syrphidea.

6. Review of the classification of the Schizophora

6.1. Preliminary remarks

The classification of the Schizophora has long been recognized as presenting formidable difficulties, not the least of which is the sheer number and diversity of the species and species-groups included. Conventionally the group has been divided into two "sections", the Acalyptratae and Calyptratae. The current delimitation of these "sections" was worked out by Girschner (1893), whose work was a major advance in the field of classification. However, only the Calyptratae in Girschner's revised sense constitutes a probable monophyletic group. The "Acalyptratae" are a residual group (paraphyletic in Hennig's sense) which contains all Schizophora excluded from the Calyptratae. Such groups do not belong to the phylogenetic system. I doubt whether even adherents of other principles of classification would find the group "Acalyptratae" satisfactory, if they examined it critically. It seems of little value for purposes of identification, since I have not yet seen a key in which members of all groups of Schizophora are likely to be taken under the appropriate alternative in the couplet where the "Acalyptratae" and Calyptratae are separated. One of the consequences of my rejecting the group "Acalyptratae" is that the group Calyptratae loses relative rank because of subordination to a wider group (Muscoidea in the new sense proposed below). This does not necessitate a change of name, since the name Calyptratae carried no connotation of rank. This relative downgrading of the Calyptratae was already implied in Hennig's (1958) treatment.

Hennig (in press) refers to the work of de Meijere (1902) on the prothoracic spiracles of dipterous pupae as possibly providing grounds for

supposing that the "Acalyptratae" are monophyletic. De Meijere reported that in many Calyptratae the prothoracic spiracular horn of the pupa pierces the wall of the puparium, and evaluated this condition as plesiomorphous ("primitivste") for the Schizophora. I agree with Hennig that this evaluation seems justified by the data presented. However, I do not see how the "Acalyptratae" can be characterized by synapomorphous reduction of the spiracular horn ("äusseres Tüpfelstigma"). De Meijere reported that the spiracular horn also pierces the puparium in some Heleomyzidae (*Leria* and *Heleomyza*), and the possibility that such a condition occurs more widely among "Acalyptratae" cannot be excluded, as representatives of only a few families were examined.

Hennig's (1958) work was the starting point of my present study. In that work Hennig reviewed previous proposals for the classification of the Schizophora, and presented a revision based on his own analysis of certain character sequences (mainly involving the chaetotaxy of the head and the wing venation). Hennig's classification has a provisional appearance. Some of his proposed superfamilies were stated to be tentative and weakly based, and many families were not placed in any superfamily but treated as "families of uncertain relationships". Hennig's acknowledgement of the inconclusive results of his analysis in some areas of the system is commendable, since he largely resisted the temptation of proposing groups on too speculative a basis for the sake of achieving a more satisfying formal presentation of the system. Some of the uncertainty which attends the results of Hennig's analysis is due to the nature of the character sequences chosen. The modifications of wing venation shown by the Schizophora mostly involve relatively minor changes which have occurred independently in many different groups. Similar changes in the chaetotaxy of the head also occurred

independently in different groups, and the frequency of individuals with abnormal frontal chaetotaxy in many species clearly suggests that some modifications of this chaetotaxy (such as changes in the number of orbital bristles) may involve little genetic complexity. Because of difficulties in separating true synapomorphies from the numerous homoplastic similarities shown in these character sequences, Hennig was only able to propose a few groups above the family level which he considered to be firmly based. The need to widen the scope of Hennig's analysis by incorporating additional characters is clear. In this study I have incorporated characters of the male postabdomen and genitalia into the analysis. Hennig (1958) used characters of the male postabdomen to a limited extent, but some of his characterization is not sufficiently explicit. In particular, his statements that only a single dorsal sclerite is present between the preabdomen and the hypopygium in some families do not explain the homology of the sclerite and the nature of the character sequence which has led to this condition. These comments on the limitations of Hennig's work are not intended as criticisms. For the Schizophora are such a large and diverse group that restriction of the characters analysed is necessary, if a comparative study is to be completed within a reasonable length of time. For this same reason my own investigations have been largely restricted to a limited range of characters (involving the structure of the male postabdomen and external genitalia). Undoubtedly there are other characters which, if analysed comprehensively, could be used to improve the classification. The structure of the female postabdomen and reproductive system is an obvious example.

The above remarks on restriction of the characters which I have analysed do not mean that I propose a classification based solely on

these characters. All groupings suggested by my new data have been tested for compatibility with other character sequences already analysed in the literature (both in Hennig's works and elsewhere), and in principle I admit no restriction of the range and kind of characters which should be considered. If I do not discuss certain characters used in taxonomic descriptions, this is because they have not been sufficiently analysed from an evolutionary point of view.

My interpretations of the characters analysed by Hennig (1958) follow, with few exceptions, those given in that work. It is possible that Hennig's interpretation of two characters, the development of the costa and postvertical bristles, should be reversed in some cases (e.g. in the Micropezoinea): for the suggested apomorphic conditions (costa broken; postverticals convergent) are at least as widely distributed as the conditions which Hennig considers usually plesiomorphic (costa unbroken; postverticals divergent). This question is complicated because these character states must on any reasonable interpretation be postulated to have changed independently in several different lineages, possibly with reverse changes in some cases. On balance I have decided not to reappraise extensively characters apart from the male postabdomen and genitalia. I think it preferable to see how well my interpretation of this character complex stands the test of criticism, before using it as a yardstick to test the compatibility of other workers' interpretations of other characters.

The assignment of formal rank in the system here presented is provisional, because the available historical information is too little to apply the criterion of age of origin to the ranking of particular groups. The Jurassic deposits from Kazakhstan studied by Rohdendorf and his collaborators have not yielded any Cyclorrhapha, but the material described from

them includes *Protempis* (Protempididae), which is possibly referable to the stem-group of the Eremoneura (see section 4). If this is so, then these deposits preceded the age of origin of the Schizophora. The earliest fossil Schizophora so far reported are an undescribed specimen in Canadian amber believed to be of Late Cretaceous age (listed as a chloropid by J. F. McAlpine and Martin 1969) and some puparia tentatively referred to the Calliphoridae (J. F. McAlpine 1970) from the Edmonton Formation (Alberta) of latest Cretaceous age. These meagre finds provide no basis for applying Hennig's (1966a: 186) proposal that in classifying insects the boundary between the Upper and Lower Cretaceous can be taken as the boundary between the family level and lower levels. Consequently it is impossible to say that authors who have treated the Schizophora as consisting largely of a single family "Muscidae", such as Lameere (1906), are wrong in any formal sense. At present we cannot apply any guidelines to settle this question. My approach in these circumstances has been, in general, to disturb minimally the ranks conventionally assigned to taxa. As a result some discrepancy has been accepted between the sequence of subordination indicated by my analysis and the categorical ranks formally assigned. This discrepancy manifests itself in my arrangement of some families in "family-groups", which would be ranked only as families according to the sequence of subordination (see table 2).

I propose to introduce into the classification of the Schizophora a category between superfamily and family, indicated by the suffix "-oinea". This follows the proposal of von Kéler (1963: 636), who uses the name "suprafamilia" (German: "Oberfamilie") for such a category. However, the prefix "supra-" is merely a variant of "super-" and does not seem sufficiently distinctive. I propose therefore to substitute the prefix "prae-"

("pre-" in English), so that the category name becomes prefamily (or praefamilia in Latin). If my proposal gains acceptance, similar changes should be made to the Latin and English names of other categories for which von K  ler uses the prefix "supra-". According to my revision of von K  ler's proposals the complete list of family-group categories is as follows: superfamily, prefamily, family, subfamily, infrafamily. Between the family-group and order-group von K  ler interposes the phalanx-group, to which I refer the taxa Eremoneura, Cyclorrhapha and Schizophora (see table 2). The use of so many intermediate categories between family and order will doubtless be deprecated by some. But in relation to the numbers of species classified, the numbers of categories used is not unusually high. Of course the full list of categories given by von K  ler should not be regarded as mandatory, for the use of so many categories would be superfluous in classifying less diverse groups of organisms.

Rohdendorf (1964) has classified the Diptera on different principles from those followed in this work. The taxa in his system are based directly on conformity with particular functional-morphological types, and are not intended to represent monophyletic groups in all cases. Rohdendorf's classification should therefore be considered a morphological-phenetic classification, and should not be confused with the phylogenetic system which I discuss in this work. Consistent with his principles of classification Rohdendorf accords high formal rank to certain highly modified groups, notably the Termitoxeniinae ("infraorder Termitoxeniomorpha"), the Braulidae ("infraorder Braulomorpha") and the groups which I include in the Hippoposcidae family-group ("infraorder Nycteribiomorpha", "infraorder Streblomorpha", "superfamily Glossinidea", "superfamily Hippoboscidea"). In a phylogenetic system these groups should be given lower rank because of

their position in a sequence of subordination which is determined, at least in a relative sense, by the time dimension (see section 2.1). Both treatments are formally correct within the framework of the type of classification followed, and the striking differences which result from applying different principles of classification do not necessarily indicate differing opinions about either the phylogenetic relationships or morphological divergence of the groups concerned. However the subdivision of the "infraorder Myiomorpha" (including most Schizophora) in Rohdendorf's classification seems to me unduly arbitrary, and many of the included superfamilies are insufficiently characterized. I doubt whether some of these proposed superfamilies would stand the test of more critical analysis even in terms of Rohdendorf's own principles of classification. For instance, his "superfamily Borboridea", containing the Agromyzidae, Milichiidae, Sphaeroceridae (= Borboridae) and Cryptochetidae, is a highly heterogenous group, both from the standpoint of phenetic and phylogenetic classification. Because Rohdendorf does not classify in accordance with the principles of phylogenetic systematics, many of his group names do not refer to groups in the phylogenetic system, and are consequently not used in the classification presented in this work.

The classification presented here is a classification of existing groups, and I have not attempted to review the fossil forms. Hennig's (1965b, 1967, 1969b) fine works on the Baltic amber fauna provide the main body of useful information on fossil Schizophora. Much of the material preserved in other media is in too poor condition to be of much value for evolutionary studies, although this has not deterred some authors from naming numerous specimens of doubtful significance.

At a late stage in the preparation of this work I received two

important papers dealing with the classification of the Schizophora, and revised my manuscript to take account of these. The first was Speight's (1969) work on the prothoracic morphology of "acalypterates". Speight offered only a few firm conclusions on the relationships of the families, because he found that few of them could be characterized by apomorphous conditions of the prosternum. His work is marred in some places by confused argumentation and is consequently criticized in the paper by Hennig discussed in the next paragraph. But on the whole it is a helpful contribution to our knowledge of the Schizophora, and the range of material studied (2150 species) is unusually extensive.

I also received at a late stage of this study a manuscript copy of a paper by Hennig entitled "Neue Untersuchungen über die Familien der Diptera Schizophora". This is a supplement to his 1958 paper, and includes some important new information and discussion on Drosophiloidea and Anthomyzoina. Hennig's manuscript was ready for press at the time I sent him a preliminary draft of my manuscript for comment. He decided that the best procedure would be to let his paper go to press without substantial alteration, while making the manuscript available to me so that I could take account of it in completing my manuscript. At the time of writing (March 1971) Hennig's paper is still unpublished.

Morphological foundations of superfamily classification

In the section which follows (6.2) I present a classification of the families of Schizophora in five superfamilies: Lonchaeoidea, Lauxanioidea, Drosophiloidea, Nothyboidea and Muscoidea. Some of the characters on which this classification is based are indicated on figure 14. In this thesis I restrict my discussion to the superfamilies and prefamilies, but a lengthier version with descriptions and discussion of each family will be

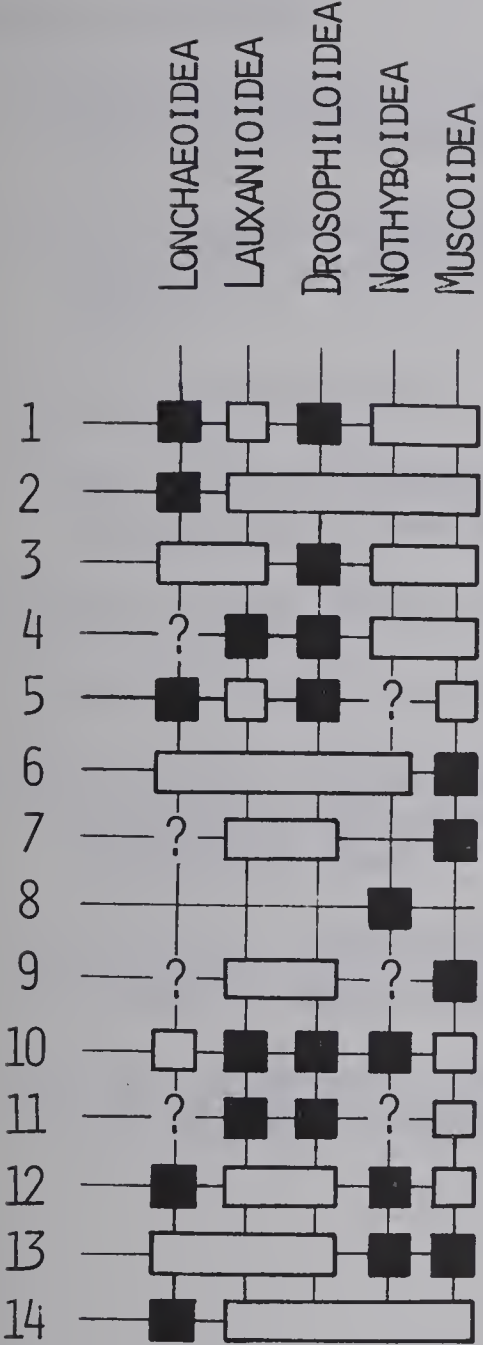


Fig. 14. Distribution of some character states among the superfamilies of Schizophora

Apomorphous conditions
(black rectangles)

Plesiomorphous conditions
(white rectangles)

Head

- 1. 2nd antennal article with cleft
- 2. Only 1 ors present
- 3. Proclinate ors present
- 4. Postverticals convergent

- 2nd antennal article without cleft
- At least 2 ors present
- Proclinate ors absent
- Postverticals divergent

Wing

- 5. Costa broken at end of sc

- Costa unbroken

(Cont'd)

Fig. 14 (Cont'd)

Male postabdomen

- | | |
|--|---|
| 6. 6th sternum more strongly developed on left side | 6th sternum symmetrical |
| 7. 7th sternum asymmetrical, extending dorsally on left side | 7th sternum symmetrical |
| 8. 7th sternum lost | (as 7) |
| 9. 7th tergum reduced to lateroventral vestige | 7th tergum well developed in dorsal position |
| 10. 8th tergum vestige lost | 8th tergum vestige present |
| 11. 8th sternum reduced or lost | 8th sternum large |
| 12. Aedeagal apodeme linked to hypandrium or body wall between hypandrial arms | Aedeagal apodeme free from hypandrium and body wall |
| 13. Aedeagus swung through wide arc against aedeagal apodeme | Aedeagus without well developed swinging mechanism |
| 14. 7th tergum and sternum fused; 8th segment elongate | 7th tergum and sternum discrete; 8th segment short |

published.

I will explain the grounds for my proposing a revised superfamily classification first by discussing the Drosophiloidea and Muscoidea, leaving aside for the moment the other three superfamilies since ontogenetic information on them is not yet available. The Muscoidea and Drosophiloidea show in their groundplans gross structural differences in the male postabdomen, which are analysable into an alternance of apomorphous and plesiomorphous conditions. In the groundplan of the Muscoidea the sclerites of the 8th segment are developed as in the Platypezidae (figs. 10 - 11), with a large inverted sternum in dorsal position and reduced ventral tergum. In this respect the Muscoidea are relatively plesiomorphous, since in the Drosophiloidea the sclerites of the 8th segment are vestigial or absent in the male. However, the Drosophiloidea are relatively plesiomorphous in respect of the sclerites of the 7th segment, which in the groundplan of the group are fully or nearly symmetrical plates in dorsal and ventral positions. In Muscoidea the 7th tergum is never developed as a symmetrical dorsal plate, but is asymmetrically reduced to a vestige situated lateroventrally on the right side in the groundplan of the group. Because of this alternance of relatively plesiomorphous and apomorphous conditions, I think it would be unwarranted to maintain that either type of structure was derived from the other; more probably both types are independent modifications of the type of structure shown by the Platypezidae. As a result of new information now available on the development of the genital discs in Muscoidea (Dübendorfer 1970), I can reinforce this conclusion with ontogenetic evidence. It now seems likely that the differences in post-abdominal structure between the Drosophiloidea and Muscoidea rest on

differences in the ontogenetic process which can be traced back to the blastoderm stage of the embryo, when the imaginal presumptive areas are determined (see Anderson 1966). In order to make this point clear, I set out the relevant data in table 3. I use *Mycetophila* as the starting point of the comparison, since this is probably the most closely related to the Brachycera (of which the Cyclorrhapha are a subordinate group) of the non-brachycerous groups for which relevant information is available (see Hennig 1968b). The larva of *Mycetophila* resembles that of the Cyclorrhapha in showing a series of imaginal discs on all abdominal segments (Abul Nasr 1950), but there are three pairs of discs on each segment, compared with only two pairs in the cyclorrhaphous Tephritidae (Anderson 1966).

If the position and development of the imaginal discs in the Muscoidea is compared with that in *Mycetophila*, it seems likely that the lateral genital discs of Muscoidea are homologous (at least in part) with the ventral discs of the 8th abdominal segment in *Mycetophila*. However, the lateral genital disc of Muscoidea generates structures in addition to those generated by its equivalent in *Mycetophila*, so that an increase of the field which the discs are capable of generating or coalescence of previously separate discs must be postulated. The same applies to the median genital disc of Muscoidea, which generates the proctiger (including the cerci) and proctodaeum (hind gut), in addition to structures homologous with those generated by the ventral median discs of *Mycetophila*. In *Mycetophila* the sclerites of the proctiger develop from two additional pairs of discs, while the proctodaeum is not reported to develop from any disc. But it is important to note that the genital arch (8th tergum) in female *Drosophila* is not generated by the genital disc. I think it

Table 3. Development of imaginal discs in Bibionomorpha and Brachycera.

	Imaginal discs on larval 8th and 9th abdominal segments (<i>Mycetophila</i>) or 8th abdominal segment (<i>Cyclorrhapha</i>)		Imaginal structures which the discs generate	
			♂♂	♀♀
<i>Mycetophila</i> (Bibionomorpha, <i>Mycetophilidae</i>) (after Abul Nasr 1950)*	8th larval segment	ventral discs	not established	Vagina, spermathecae and common oviduct
		lateral discs	not established	not established
		dorsal discs	not established	not established
	9th larval segment	ventral median discs	9th sternum, parameres, aedeagus, paraphyses and ejaculatory ducts	caecus (parovaria)
		lateral discs	10th sternum (hypoproct)	10th sternum
		dorsal discs	cerci	cerci
Tephritidae and Calyptratae (<i>Cyclorrhapha</i> , <i>Muscoidea</i>) (after Anderson 1966, Black 1966 and Dübendorfer 1970)	lateral genital discs		8th sternum (? also 8th tergum, when present)	8th tergum and 8th sternum, vagina, spermathecae and common oviduct
	median genital disc		all external structures of genital (9th) segment, ejaculatory duct, accessory glands (paragonia), proctiger and proctodaeum (hind gut)	parovaria, proctiger and proctodaeum (hind gut)
<i>Drosophila</i> (<i>Cyclorrhapha</i> , <i>Drosophiloidea</i>) (many references)	median genital disc		all external structures of genital (9th) segment, ejaculatory duct, accessory glands (paragonia), proctiger and proctodaeum (hind gut)	vaginal plates (8th sternum), vagina, spermathecae, common oviduct, parovaria, proctiger and proctodaeum (hind gut)

(Cont'd)

Table 3 (Cont'd)

*There are certain differences between Abul Nasr's (1950) terminology and that which I use in this work. The structures which Abul Nasr calls "gonapophyses" are what I call parameres: he applies the term "parameres" to some kind of paraphyses (possibly homologous with the postgonites of the Cyclorrhapha). I do not accept his homology of the cerci with the "10th tergum". He describes biarticled cerci in the female of *Mycetophila*, as also in the groundplan of the Brachycera (see Herting 1957). Abul Nasr did not clarify the origin of the 9th tergum in either sex. Therefore, his suggestion (his page 381) that the imaginal terga are derived from discs (or buds) is not proven. I interpret Abul Nasr's figures as indicating that the true 10th tergum is absent in both sexes of *Mycetophila*. Since this sclerite is retained in the groundplan of the Brachycera (in both sexes), it is possible that there are some differences between the pattern of imaginal discs shown by *Mycetophila* and that shown in the groundplan of the Brachycera. However, in the absence of relevant information on any group of Brachycera whose postabdominal morphology is close to the groundplan condition, I can only use the information on *Mycetophila* for purposes of comparison.

improbable that the median genital disc of *Drosophila* was derived through coalescence of discs from the condition shown by the Muscoidea, for in the Muscoidea the structures generated by the lateral genital discs include the 8th tergum. More probably the conditions shown by the Muscoidea and Drosophiloidea were not either derived from the other, but are independent modifications of some earlier condition, in conformity with the conclusion reached above from considerations of comparative morphology.

Where then do the Lonchaeoidea, Lauxanioidea and Nothyboidea fit into this picture? For the present I leave open the question of whether each of these groups is more closely related to the Drosophiloidea or to the Muscoidea. The arrangement of the male postabdominal sclerites in the Lauxanioidea and Nothyboidea may agree with that in the groundplan of the Drosophiloidea (with the 7th tergum retained in dorsal position, but with the sclerites of the 8th segment lost). However the homologies of the sclerites concerned have not been critically demonstrated, and I therefore do not think that the evidence is sufficient for formally grouping them with the Drosophiloidea. A particular problem arises in interpreting the relationships of the Nothyboidea. This group shows in its groundplan the characteristic mechanism for swinging the aedeagus through a wide arc against the aedeagal apodeme to an anteriorly directed rest position, as in the Muscoidea. If the Nothyboidea are more closely related to the Drosophiloidea and Lauxanioidea than to the Muscoidea, then possibly the swinging mechanism has been secondarily lost in the Drosophiloidea and Lauxanioidea. On present information I doubt whether the latter hypothesis is correct, since the aedeagus of some Lauxanioidea (especially Chamaemyioinea) is upcurved and uniformly sclerotized, as I postulate for the groundplan of the Schizophora (compare the types of aedeagus shown by the Lonchaeoidea and

Platypezidae). However, this question is not likely to be settled until comparative information is available on the imaginal discs and their development in each of the groups of Schizophora recognized as superfamilies in this work. I regard the extension of studies on the imaginal discs to a wider range of groups than hitherto as of the highest importance for clarifying the evolution of the Schizophora, and indeed of the Brachycera as a whole.

Both in *Mycetophila* and in those Cyclorrhapha which have been studied the arrangement of imaginal discs is initially the same in both sexes. This gives grounds to expect that structural differences between the females of Muscoidea and Drosophiloidea will be found to result from the different ontogenetic processes. So far little detailed comparative information on the structure of the female postabdomen is available for groups other than the Calyptratae. Wider comparative studies in this field would be of much interest.

6.2. Treatment of subordinate groups to the prefamily level

Superfamily Lonchaeoidea

My proposal of this group breaks with tradition. I include in the Lonchaeoidea two families, the Lonchaeidae and Cryptochetidae, which have usually been dissociated and placed in different family groups.

The Lonchaeidae have usually been grouped with the "Pallopteridae", which are referred in this paper to the Tephritidae s.l. (Muscoidea, Tephritoinea). Hennig (1948a) argued that such treatment was erroneous, but reverted to grouping the Lonchaeidae with the Pallopteridae in his 1958 paper. The resemblances between Pallopteridae and Lonchaeidae suggested as

synapomorphous by Hennig (1958) are: (1) the formation of an ovipositor sheath (♀) by the completely sclerotized 7th segment, (2) 6th sternum (♀) with anteriorly directed apodeme, (3) the presence of only a single pair of upper fronto-orbital bristles (*ors*), and (4) aedeagus (♂) tubular. However, there are serious obstacles to the inclusion of the Lonchaeidae in the Tephritoinea. The aedeagus of the Lonchaeidae can hardly be considered synapomorphous with that of the Tephritoinea, since it is a rigid, uniformly sclerotized structure, not flexible and extruded by pressure of body fluid as in the latter group. The development of the male post-abdominal sclerites in the groundplan of the Lonchaeidae seems to indicate that the family is not referable to the Muscoidea. Hennig's (1958) assumption that the postabdominal morphology of *Protearomyia obscura* (Walker) (which has strongly asymmetrical 6th and 7th sterna similar to the condition shown by most Muscoidea) was relatively plesiomorphous for the Lonchaeidae, is not supported by the more detailed analyses subsequently available (J. F. McAlpine 1962b, Morge 1963 and 1967). It is now clear that the groundplan of the family should include a rather large, symmetrical 6th sternum and a weakly asymmetrical 7th sternum, which (unlike in Muscoidea) was not fused with the inverted 8th sternum. A large unmodified 6th sternum is shown by all Dasiopinae, and some species of that group also retain a discrete 6th tergum. Clearly the conditions of the 6th segment shown by the Dasiopinae are more plesiomorphous than those shown by the Lonchaeinae s.l., as stated by Morge (1963). The development of the 7th sternum is variable in both subfamilies, and some degree of asymmetry may probably be ascribed to the groundplan of the family. However this asymmetry is weak in many groups, as indicated for instance by McAlpine's (1962b) figures of *Dasiops relictus* McAlpine (fig. 32) and *Lonchaea subpolita* Malloch

(fig. 38). There is no indication in the structure of Lonchaeidae of the asymmetrical reduction of the 7th tergum characteristic of the Muscoidea, where this sclerite is represented only by a vestige on the right side (near the 7th right spiracle). Probably McAlpine and Morge are correct in assuming that the 7th tergum is represented by the last distinct dorsal sclerite, which is symmetrical or, if asymmetrical, more strongly developed on the left side. The fate of the sclerites of the 8th segment requires clarification. A small ventral sclerite which probably represents the 8th tergum vestige is often present (called "secondary sclerite" by McAlpine 1962b). No discrete 8th sternum (inverted) has been reported in Lonchaeidae, and McAlpine (1962b: 33) interprets the structure of certain groups of *Dasiops* as indicating that this has been fused with the 7th tergum.

The evidence of the structure of the male postabdomen and genitalia, as outlined above, provides no firm grounds for including the Lonchaeidae within the Muscoidea, let alone in a close relationship with *Palloptera* (Tephritoinea). Males of the latter genus are characterized by a flexible aedeagus which is extruded by pressure of body fluid, and by loss of both pairs of postabdominal spiracles. This combination of apomorphic conditions indicates that *Palloptera* belongs to the Tephritidae family-group (Tephritoinea). Male Lonchaeidae do not show these conditions, but always retain a rigid aedeagus and the complete complement of seven pairs of spiracles.

From the above considerations I think that the hypothesis of a sister-group relationship between the Lonchaeidae and "Pallopteridae" should be definitely rejected, as the evidence of synapomorphy in the structure of the male postabdomen between *Palloptera* and other members of the Tephritidae

family-group is overwhelming. If, as seems probable, the presence of an anteriorly directed apodeme on the female 6th sternum is not a groundplan condition of the Tephritidae family-group, then the presence of such an apodeme in *Palloptera* can only be homoplastic with the similar condition shown by the Lonchaeidae. A modified version of the above hypothesis has been presented by McAlpine (1962b: 69), whose dendrogram indicates the Lonchaeidae as the sister-group of the Tephritidae family-group as a whole (= Otitoidea + Pallopteroidea). This view depends on the interpretation that certain similarities in the structure of the 7th and 8th segments of the female postabdomen in Lonchaeidae and Tephritoinea are synapomorphies. Even this view conflicts seriously with the evidence of the male postabdomen and genitalia, which provides no basis for classifying the Lonchaeidae in the Muscoidea (as previously discussed). Detailed comparative studies of the structure of the female postabdomen among the families of Schizophora are unfortunately not yet available, and such studies will possibly show that the resemblances between the Lonchaeidae and Tephritoinea are not so close as has been supposed. I have not attempted detailed comparison in the course of this study, but it may be useful for me to draw attention to one structural difference. In Lonchaeidae the sclerites of the 7th segment extend as flexible rods on the posterior part of the segment which is invaginated when the 8th segment is retracted. In the extended position these rods are seen to extend to the apex of the 7th segment, where they meet the sclerites of the 8th segment (see character 4 below). In all the preparations of Tephritoinea which I have examined, the invaginated area is membranous, so that in extended position the sclerites of the 7th and 8th segments are seen to be well separated by membrane. At any rate I postulate that the resemblances in the structure of the female postabdomen

between the Lonchaeidae and the Tephritidae s.l. rest on convergence, because of the incompatibility of their interpretation as synapomorphies with the evidence of other characters. If any authors continue to maintain that the structural similarities of the female postabdomen of the Lonchaeidae and Tephritidae s.l. (or any part of this group) are due to synapomorphy, then they should explain how this interpretation can be reconciled with the evidence of the male postabdomen and genitalia.

Hennig's (1958: 607) remarks on the possession of elongate spermathecae by *Palloptera* and the Piophilidae s.l. seem to imply that the Lonchaeidae share this apomorphous condition with these groups. However it is doubtful whether elongate spermathecae can be ascribed to the groundplan of the Lonchaeidae or of the Tephritidae family-group, since both groups contain genera with orbicular spermathecae (*Daslops* in the case of the Lonchaeidae, as indicated by McAlpine 1962b).

The only other family which can probably be associated with the Lonchaeidae is the Cryptochetidae, a small group of highly modified flies whose larvae develop as internal parasitoids of Coccidae (Hemiptera). Hennig (1958) treated the Cryptochetidae as a family of uncertain relationship. He suggested that their affinity probably lay with the Drosophiloidea, although admitting that the evidence was not really convincing. But he now definitely rejects this interpretation (Hennig, in press). I can find in the literature no strongly held opinion on the relationship of the Cryptochetidae to other Schizophora.

The larvae of Cryptochetidae exhibit a wealth of autapomorphous conditions, but the morphological gaps between them and all other known larvae of Cyclorrhapha are so great that one cannot judge the relationship of the group from characters of the larvae and puparium. Hennig (1952a: 126)

has drawn attention to an interesting similarity between the Cryptochetidae and Platypezidae in respect of the position of the ecdysial sutures on the puparium. It is not clear whether this is a plesiomorphous condition in the Cryptochetidae or has evolved secondarily.

A case can be made on the basis of adult morphology for grouping the Cryptochetidae with the Lonchaeidae, with whom they share certain distinctive apomorphous conditions, notably involving the structure of the antennae and the development of a dense coat of setulae over most of the body.* Both the Lonchaeidae and Cryptochetidae exhibit a similar type of aedeagus (upcurved, with uniform sclerotization, without any swinging mechanism), a plesiomorphous condition for the Schizophora (see also section 3.1) which seems to exclude the possibility of a close relationship between these families and the Drosophiloidea. A similar type of aedeagus is shown by some Lauxanioidea, but clear synapomorphies between that group and the Lonchaeoidea are lacking. Hennig's (1948a) view that the Lonchaeidae were closely related to the Chamaemyiidae (Lauxanioidea) was subsequently abandoned by him (Hennig 1958). Another probable symplesiomorphous condition of the Lonchaeidae and Cryptochetidae is their retention of uniformly dark body colour with dark halteres. In this respect they resemble the Pipunculidae (Syrphidea), Platypezidae and Hypocera. Hennig (1967) originally stated that the Baltic amber species *Morgea mcalpinei* Hennig had pale halteres, but his remarks on a second specimen (Hennig 1969b) indicate that the halteres of this species were probably infuscated in life.

The Lonchaeoidea in the sense here proposed may be characterized by the following apomorphous conditions with respect to the groundplan of the Schizophora:

- (1) 2nd antennal article with longitudinal cleft or suture;

*If these grounds are considered insufficient for formally classifying the Cryptochetidae in the Lonchaeoidea, then that family can only be added to the list of Schizophora of uncertain position. There are no grounds for including it in any other superfamily.

3rd article downwardly directed with subbasal arista (see Hennig 1965b: 178 and J. F. McAlpine 1962b: 18).

Similar conditions occur through convergence in the Calyptratae, some Tephritidae s.l. (Tephritoinea), *Loxocera* (Psilidae) and most Drosophiloidea. While recent Cryptochetidae have highly modified antennae (entirely lacking the arista), the Baltic amber fossil *Phanerochaetum* described by Hennig (1965b) has similar antennae to those of some Lonchaeidae.

- (2) Only one upper fronto-orbital bristle (*ors*) present, on short vertical plates.

I list this character as apomorphous following Hennig (1958). It seems clear from Hennig's analysis that at least two pairs of orbital bristles were present in the groundplan of the other superfamilies of Schizophora, and that the presence of only a single pair in some members of these superfamilies should be considered apomorphous. Only the Lonchaeoidea contain no species with any indication of a second pair of orbitals. It is difficult to judge whether the presence of only a single pair of orbitals in the Lonchaeidae is primary, that is inherited from the groundplan of the Schizophora, or is an autapomorphous condition of the Lonchaeoidea. On balance, I accept Hennig's evaluation of this condition as apomorphous as the more probable interpretation, since two pairs of fronto-orbitals are present in members of the non-schizophorous groups Platypezidae and Hypocera.

The frons in Lonchaeoidea is covered by an extensive coat of setulae. Postvertical bristles are poorly differentiated from the surrounding setulae, and their homology with the postverticals of other Schizophora requires clarification. J. F. McAlpine (1962b) refers to two pairs of postverticals, one convergent and one divergent, in some Lonchaeidae. It is not clear whether such a condition should be considered apomorphous or plesiomorphous with respect to the groundplan of the Schizophora.

- (3) Costa broken at end of subcosta.

- (4) 7th abdominal segment (♀) with tergum and sternum broadly fused anteriorly, forming oviscape (basal cone of ovipositor); tergum and sternum extending as pairs of flexible rods on posterior half of this segment, which forms eversible sheath for 8th segment when the latter is retracted within oviscape; 8th segment elongate ("the main shaft of the ovipositor", J. F. McAlpine 1962b), with tergum and sternum both modified to form pairs of slender rods.

Both McAlpine and Morge have interpreted the eversible sheath in Lonchaeidae as representing the 8th segment, and the shaft of the ovipositor as representing the 9th segment. I think this incorrect, as the female gonopore is situated on the posterior margin of the 8th segment in Diptera. The probable explanation of this discrepancy in segment numbering is that the eversible sheath does not constitute a separate segment.

The above characterization refers to the condition shown by the Lonchaeidae. In Cryptochetidae the 7th and 8th segments are membranous. Thorpe (1934) describes the 7th segment as "membranous with incompletely defined tergum and sternum and . . . covered with minute backwardly projecting spines". The evolution of internal parasitism by the Cryptochetidae has doubtless been accompanied by profound changes in the structure of the ovipositor. The condition in Cryptochetidae was possibly derived from the condition shown by Lonchaeidae through reduced sclerotization and modification of the hairs which this segment bears in Lonchaeidae to form the "spines".

(5) Dorsal sclerites of 7th and 8th abdominal segments reduced

(♂) (figs. 18 and 22).

In Lonchaeidae a narrow dorsal pregenital sclerite lies between the 6th tergum and the periandrium. This sclerite is free in *Dasiops*, but is partly fused with the 6th and 7th sterna in other genera (J. F. McAlpine 1962b). It is not clear whether this sclerite represents the 7th tergum or a fusion of the 7th tergum and 8th sternum, as implied by McAlpine (1962b). In Cryptochetidae no such sclerite is present, the last dorsal sclerite before the genital segment being the large 6th tergum.

(6) Aedeagal apodeme (♂) linked with hypandrium (figs. 21 and 23).

The form of the aedeagal apodeme and hypandrium among the Lonchaeoidea is variable, and I am not able to define the groundplan condition precisely. However, some form of fusion or connection between the hypandrium and aedeagal apodeme is common to all members of this group. In Cryptochetidae the connection takes the form of a long process ("Medianfortsatz der Tragplatte", Hennig 1937b). In all Lonchaeidae the aedeagal apodeme is partly fused with the hypandrium (at most with its anterior end free in *Dasiops*).

Combined with their characteristic apomorphic features (as listed above), the Lonchaeoidea show several plesiomorphous conditions which suggest that they early became separated from the other groups of Schizophora. In the males of many Lonchaeidae, a complete series of ventral postabdominal sclerites is retained (fig. 20), including the 7th sternum (which retains *sensilla trichodea* like the preceding sterna) and the inverted 8th tergum

(called "secondary sclerite" by J. F. McAlpine 1962b). Outside the Lonchaeidae the only Schizophora which retain the latter sclerite are certain Muscoidea. The type of aedeagus shown by the Lonchaeoidea seems hardly different from that of the Platypezidae, and I consider it to be close to the groundplan condition for the Schizophora. In both Lonchaeoidea and Platypezidae the aedeagus is normally uniformly sclerotized, expanded at its base, but becoming slender and upcurved along most of its length. The aedeagus is directed more or less posteriorly in relation to the longitudinal axis of the insect, and cannot be "swung" against the aedeagal apodeme to any significant degree. In some Lonchaeidae the aedeagus is divided into two sections through a break in the sclerotization, but this seems to be an apomorphic condition (as stated by Morge 1963), not attributable to the groundplan of the family. The extremely short aedeagus of some groups of *Dasiops* is probably also apomorphic. Consistent with my interpretation of the early separation of the Lonchaeoidea from other Schizophora, I accept the uniformly dark coloration and dark halteres of this group (as in Pipunculidae, Platypezidae and Hypocera) as a plesiomorphous condition retained from the groundplan of the Schizophora.

Particularly interesting is the prevalence of synorchesic swarming among male Lonchaeidae. Correlated with this behaviour are certain structural peculiarities such as enlarged male eyes and strong anal lobes on the wings. This subject has been ably reviewed by J. F. McAlpine and Munroe (1968), who conclude that "the synorchesic swarming habit in Lonchaeidae is believed to be evidence of the primitive nature of this family in relation to most other Acalypteratae". Their view is that the swarming habit and the associated structural peculiarities were derived from ancestors of the Schizophora and not

secondarily acquired after differentiation of the Schizophora had begun. This interpretation seems to me very probable, and accords well with the early separation of Lonchaeoidea suggested by the morphological evidence. I therefore postulate that the structural features associated with synorchesic swarming in Lonchaeidae, such as enlarged male eyes and large anal lobes on the wing, are groundplan conditions for the Schizophora which have been retained by this family. Among other superfamilies of Schizophora pronounced sexual dimorphism in the size of the eyes occurs only among three groups of Muscoidea, the Calyptratae, the Tanypteroidea and *Neomaorina* (Tephritidae family-group), and also in the lauxaniid genus *Holopticaender* (Hennig 1968a). The view that synorchesic male swarming was a plesiotypic habit of the Cyclorrhapha is further supported by the prevalence of this habit among the Platypezidae, which seem to be the least modified of all recent Cyclorrhapha (especially in respect of the morphology of the male postabdomen and the partial reversibility of the circumversion process). The eyes are always contiguous in male Platypezidae (Kessel and Maggioncalda 1968a).

Superfamily Lauxanioidea

My delimitation of the Lauxanioidea follows that of Hennig (1958), except that I exclude the Periscelididae (here referred to the Nothyboidea). Hennig (in press) now also excludes the latter family from the Lauxanioidea. The Lauxanioidea in my present sense consists of two well-characterized subordinate groups, here accorded prefamily rank (Lauxanioidea and Chamaemyioidea). I am reasonably confident that each of these groups is monophyletic. But their association in the Lauxanioidea rests on weak characterization and may be incorrect. Hennig (in press) also alludes to

this possibility, stating that only the Lauxaniidae and Celyphidae belong with certainty to the Lauxanioidea. My retention of the group Lauxanioidea in a wide sense is therefore provisional and in need of confirmation (or refutation) through further studies.

If the Lauxanioidea in the present sense are monophyletic, the group may be characterized by the following apomorphous conditions with respect to the groundplan of the Schizophora:

- (1) Postverticals (*pvt*) convergent.

The only group with long divergent postverticals included by Hennig (1958) in the Lauxanioidea are the Periscelididae, which I refer to the Nothyboidea.

- (2) Anal vein shortened, not reaching wing margin (Hennig 1958).

- (3) Only one dorsal sclerite (probably 7th tergum) between 6th tergum and periandrium (♂) (figs. 26 and 30).

The homology of this 7th dorsal sclerite is not clear. It may represent the 7th tergum, the inverted 8th sternum or a fusion of both (as interpreted by Hennig 1958). I think the first alternative the most probable, but this question may not be clarified until information is available on the ontogeny of the sclerites or on the morphology of intersexes (see section 6.1).

- (4) 8th tergum vestige (♂) lost.

Hennig (1938e) labelled the last ventral sclerite before the genital segment in *Parochthiphila* (Chamaemyiidae) as "sternite 8", but this is surely the 7th sternum.

The Lauxanioidea exhibit several features in their groundplan which are thought to be plesiomorphous. The costa is unbroken and the subcosta well developed. A complete series of ventral sterna up to the 7th sternum is present in the male, as retained by many Chamaemyiidae (fig. 28). Oral vibrissae are not differentiated. The type of aedeagus is probably similar to that of the Lonchaeoidea and Platypezidae, namely a more or less uniformly sclerotized structure, upcurved along most of its length and always directed more or less posteriorly in relation to the longitudinal

axis of the insect. No mechanism has been developed in any Lauxanioidea for swinging the aedeagus through a wide arc against the aedeagal apodeme (as is characteristic of the Muscoidea and Nothyboidea).

Prefamily Lauxanioinea

The Lauxanioinea are characterized in their groundplan by the following apomorphous conditions with respect to the postulated groundplan of the Lauxanioidea.

- (1) Male accessory glands ("paragonia") repeatedly branched, forming dense tangle (Sturtevant 1926).

Sturtevant reports this condition in all the genera of Lauxanioinea which he examined, namely *Calliope*, *Camptoprosopella*, *Lauxania*, *Minettia*, *Sapromyza* and *Steganolauxania*. He stated that the condition was not shown by members of any of the other groups (including Chamaemyiidae) which he had examined. Sturtevant's observations indicate that a major structural modification of the male reproductive system has occurred in Lauxanioinea, and I am convinced by this evidence that the Lauxanioinea are a monophyletic group.

- (2) Postgonites lost (♂).

Additional autapomorphous conditions may possibly be found in the structure of the female genital segment, since this shows unusual internal sclerotization and modification of the 8th sternum in the species which I have studied (*Sapromyza*, *Lauxania*). Further studies are needed to clarify this point. Hennig (1958) has suggested that the location of the female 7th spiracles within the 7th tergum is an apomorphous condition of the Lauxaniidae; but this is probably not a groundplan condition of the Lauxanioinea, since at least in *Sapromyza* these spiracles lie in membrane (as indicated by Hahn 1929 and confirmed by my own observation).

Plesiomorphous conditions retained in the groundplan of the Lauxanioinea include: (1) a well-developed subcosta, well separated from r_1 at its apex; (2) a large unmodified 6th tergum in the male; (3) a rod-like

aedeagal apodeme (♂), free from the hypandrium (fig. 27); and (4) three spermathecae (♀). It is doubtful whether the condition of the aedeagus in the groundplan of the Lauxanioinea can be characterized as apomorphic in any respect. Although some genera show characteristically modified types of aedeagus (including even complete reduction in *Homoneura laticosta* Thomson according to Hennig 1948a), a fairly slender and upcurved aedeagus is shown, for instance, by *Camptoprosopella* (fig. 27).

Prefamily Chamaemyioinea

I include in this group the families Eurychoromyiidae and Chamaemyiidae. The view that the Chamaemyioinea are monophyletic is supported by the following condition which I interpret as an autapomorphic groundplan condition of the group:

- (1) Four spermathecae (♀) (Sturtevant 1926, Hennig 1958).

While a reduction in the number of spermathecae from three to two has evidently occurred independently in many lineages of Schizophora, an increase in this number to four has occurred much more rarely. Outside the Chamaemyioinea four spermathecae have been reported only for two species of *Suillia* (Heleomyzidae) (Hennig 1958), *Seioptera* (Tephritidae s.l.) (Sturtevant 1925), some Conopidae and *Salticella* (Sciomyzidae) (Steyskal 1965). All these genera are clearly referable to families for which the presence of three or two spermathecae is the groundplan condition, and the evolution of the four-spermathecae condition was evidently independent in each case. However, the presence of four spermathecae in the Eurychoromyiidae gives grounds for supposing that this group is closely related to the Chamaemyiidae, as suggested by Hennig (1958), since the condition seems to belong to the groundplan of both families. Other characters of the Eurychoromyiidae are readily

compatible with this interpretation, but offer serious obstacles to classifying the group in the Sciomyzoinea.

Superfamily Drosophiloidea

My delimitation of the Drosophiloidea follows Hennig (1958). The included families are: Drosophilidae, Camillidae, Curtonotidae, Campichoetidae and Ephydriidae. Speight (1969) and Colless and D. K. McAlpine (1970) have proposed to widen this group to include the Chloropidae and various other families. I do not see sufficient justification for these proposals. The morphology of the male postabdomen of the Drosophiloidea (*sensu* Hennig) is very different from that of the Chloropidae and all other families which I refer to the Muscoidea in this work, and Hennig (in press) presents additional evidence for the monophyly of the Drosophiloidea in his sense from study of the structure of the antennae. The Drosophiloidea in Hennig's sense seem to me to be one of the most surely grounded monophyletic groups of the Schizophora, characterized in their groundplan by the following apomorphous conditions with respect to the groundplan of the Schizophora:

- (1) Proclinate fronto-orbital bristle (*ors*) present.

Hennig (1958 and 1965b: 190) has discussed the variation in this character.

- (2) 2nd antennal article with longitudinal cleft or suture (see discussion by Hennig, in press).

- (3) Aedeagus (♂) short.

The type of aedeagus in the groundplan of the Drosophiloidea cannot be defined precisely. However, since nearly all Drosophiloidea (except a few groups of Drosophilidae) show a very short aedeagus, the groundplan condition for the Drosophiloidea is probably apomorphous in this respect in comparison with the elongate condition which I ascribe to the groundplan of the Schizophora (as retained by many Lonchaeoidea and Lauxanioidea).

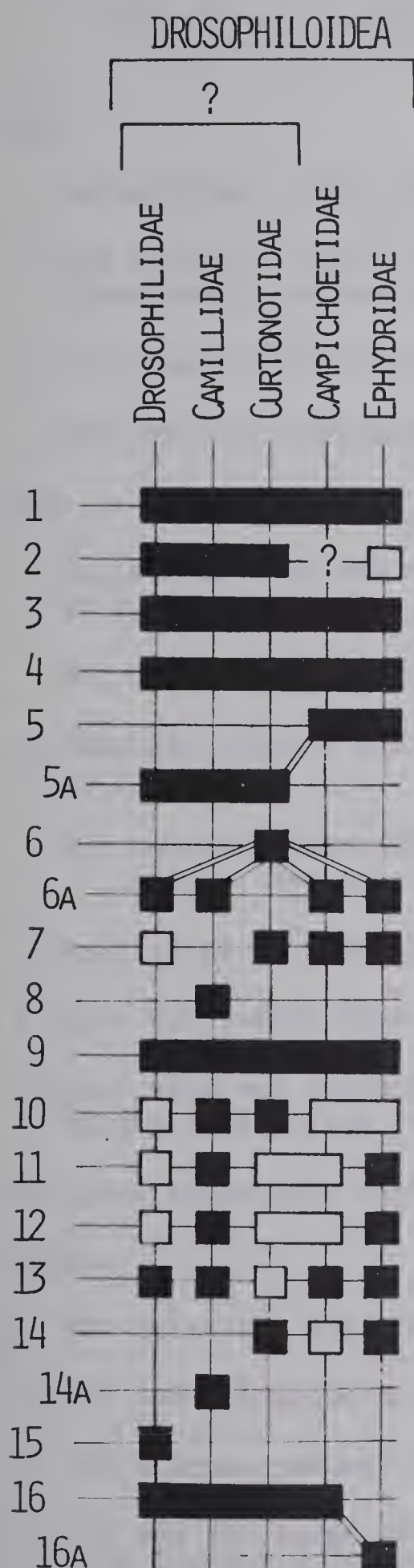


Fig. 15. Distribution of some character states among the families of Drosophiloidea. The black rectangles indicate groundplan conditions interpreted as apomorphous with respect to the groundplan of the Schizophora. Where common possession of such apomorphous conditions is interpreted as due to synapomorphy, a continuous black rectangle is shown against the families concerned. Corresponding plesiomorphous conditions are shown by the white rectangles. Further modifications of a primary apomorphous condition are shown in separate rows, with synapomorphy at the primary level indicated by linking the rectangles. The list of characters is as follows.

Fig. 15 (Cont'd)

Apomorphous conditions
(black rectangles)Plesiomorphous conditions
(white rectangles)*Head*

1. 2nd antennal article with cleft

2. 3rd antennal article with long
dorsolateral process at base3. Proclinate *ors* present

4. Postverticals convergent

3rd antennal article without long
basal process*Wing*5. Costa broken at end of sc
or r_1

5a. Costa broken twice

6. Subcosta closely approximated
to r_1 6a. Subcosta faded or fused
with r_1 distally

7. Anal cross-vein angulate

8. Anal cross-vein lost

9. Anal vein not reaching wing
margin as distinct vein

10. Lower cross-vein lost

Anal cross-vein not angulate

(as 7)

Lower cross-vein present

Abdomen

11. 7th spiracles lost (both sexes)

12. 6th sternum reduced (σ)13. 7th sternum reduced (σ)14. 6th and 7th terga reduced,
much shorter than preceding
terga (σ)14a. 6th tergum reduced; 7th
tergum lost (σ)

7th spiracles present in both sexes

6th sternum well developed (σ)7th sternum well developed (σ)6th and 7th terga well
developed (σ)

(Cont'd)

Fig. 15 (Cont'd)

15. 6th and 7th terga fused (♂) (as 14)

16. 2 spermathecae (♀)

16a. Spermathecae reduced;
ventral receptacle
sclerotized (♀)

In Drosophiloidea no mechanism has been developed for swinging the aedeagus through a wide arc against the aedeagal apodeme (contrast the Muscoidea and Nothyboidea), and the aedeagus remains posteriorly or posteroventrally directed in the rest position. Accounts of the hypopygial musculature of *Drosophila* (Gleichauf 1936; Ferris *in* Demerec 1950) do not indicate any muscle equivalent to the "*musculus phallapodemalis basiepiphallicus*" (M 36) of Salzer (1968), which in *Calliphora* swings the aedeagus out of the genital pouch to the copulatory position. The sclerotization of the aedeagus in Drosophiloidea either appears uniform, or a pair of lateral sclerites is more or less differentiated. I suggest that the term paraphalli may be applied to such lateral sclerites, although it is not clear whether they are homologous with the paraphalli of Muscoidea. Whether or not there is a phallophore in *Drosophila* requires clarification. According to Gleichauf's account the aedeagus lacks extrinsic musculature, its retraction being effected by the "*depressores penis*" which insert on the underside of the aedeagal apodeme. However, Ferris (*in* Demerec 1950) states that these muscles ("retractor muscles of the aedeagus") insert upon the "base of the aedeagus itself". The contradiction between Ferris' and Gleichauf's accounts indicates that the hypopygial musculature of *Drosophila* needs further investigation.

(4) 8th sternum (♂) much reduced; 8th tergum lost.

The identity of all abdominal sclerites as far as the 7th segment in *Drosophila* has been definitely established from study of intersexes (see Laugé 1968). The only remaining sclerites of the male which may belong to the 8th segment are the pair of small dorsolateral sclerites which lie between syntergum (6 + 7) and the periandrium (fig. 33). These can hardly be vestiges of the 8th tergum (the most frequent interpretation in the literature on *Drosophila*), since this would be expected in a ventral position in normal males with rotated terminalia. Either they are vestiges of the inverted 8th sternum, or they are neomorphous (secondary) sclerites. The former explanation is here provisionally accepted. These sclerites have so far been reported only in Drosophilidae, where they occur widely in *Chymomyza*, *Scaptomyza* and some groups of *Drosophila*. They are particularly well developed in *Drosophila picta* Zetterstedt (see Tsacas 1969, fig. 1). These sclerites are one of the first male structures to disappear in the morphological sequence from male-type to female-type intersexes which Laugé (1968) has presented. They are retained only in individuals with almost normal male morphology, including extensive rotation, and are not found in individuals in which female structures of the 8th segment develop. The morphology of intersexes is thus compatible with the view that these sclerites belong to the 8th segment, although their homology with any particular sclerite of the female has not been demonstrated conclusively, since no series of intermediate structures has been obtained.

Some authors (such as Gleichauf 1936 and Salles 1948) have interpreted the "basal phragma" on the anterior margin of the periandrium in *Drosophila* as a fused 8th tergum. But I see no evidence that this is other than an extension of the periandrium. According to Ferris (*in* Demerec 1950) muscles inserting on the telomeres originate on this phragma. These extrinsic muscles of the telomeres are part of the normal musculature of the periandrium in Cyclorrhapha.

Reduction of the sclerites of the 8th segment in males of *Drosophiloidea* has increased the sexual dimorphism of the postabdomen, since the male hypopygial structures all belong to the 9th segment, while the female external genitalia belong to the 8th segment. Thus the genital segment of each sex bears no sclerites in the other sex, with the probable exception of the small dorsolateral sclerites in some *Drosophilidae* (as noted above). Only in intersexes do large sclerites of the 8th and 9th segments occur together in the same individual. The reduction of the 8th segment in male *Drosophiloidea* may be strongly contrasted with the structure of male *Muscoidea*; in the latter the 8th segment bears a large inverted sternum, which provides attachment for one of the muscles involved in the copulatory mechanism (see Salzer 1968).

Some of the details of the above argument have so far been confirmed for *Drosophila* only, but the structure of other *Drosophiloidea* indicates that near or complete loss of the sclerites of the 8th segment has occurred among all males of the group.

(5) Costa broken at end of subcosta (or near end of r_1 when subcosta has been reduced).

(6) Subcosta closely approximated to r_1 distally.

The condition of the subcosta in the *Curtonotidae* appears to be the most plesiomorphous condition found among the *Drosophiloidea*, as indicated by Hennig (1958). In other families the subcosta becomes faded distally or fused with vein r_1 .

(7) Anal vein much shortened, not reaching wing margin.

Hennig (1958) concluded that the long apparent "anal vein" of some *Curtonotidae* is a secondary sclerotization.

(8) Postverticals convergent (Hennig 1958).

(9) Vibrissae present (see Hennig 1958).

(10) Two spermathecae (♀).

Two spermathecae have been reported as normal for *Drosophilidae* (many references), *Campichoetidae* (Hennig 1958, J. F. McAlpine 1962a) and *Curtonotidae* (Sturtevant 1926). There are two spermathecal ducts in the *Ephydriidae* (Sturtevant 1926), although the spermathecae themselves are rudimentary in this family.

An unmodified (plesiomorphous) condition of the 7th abdominal segment (♂) seems ascribable to the groundplan of the *Drosophiloidea*, with both the 7th tergum and 7th sternum retained as discrete sclerites in normal dorsal and ventral positions. The 7th tergum is well developed and discrete in

Campichoetidae (fig. 37) and also discrete (although small) in the Curtonotidae and *Diastata* (Ephydriidae). The 7th sternum is retained as a clearly defined sclerite only in Curtonotidae (fig. 39), but its *sensilla trichodea* are present also in some Drosophilidae (Wheeler 1960). In no Drosophiloidea have I found any trace of the asymmetrical reduction of the sclerites of the 7th segment characteristic of the Muscoidea. This difference in the groundplan structure of the 7th segment is important for my interpretation of how the Schizophora should be divided into superfamilies (see section 6.1).

Hennig (in press) suggests that the Drosophiloidea may be divided into two sister-groups, the "Ephydridea" ("Diastatidae" and Ephydriidae) and "Drosophilidea" (Camillidae, Curtonotidae and Drosophilidae). This subdivision may well be valid, but the question is complicated by the existence of the group for which I propose the name Campichoetidae. In this group the position of the proclinate *ors* is similar to that in the groundplan of the Ephydriidae (in which I include *Diastata*), but the modifications of the female reproductive system characteristic of the Ephydriidae are lacking. Unfortunately Hennig does not discuss members of the Campichoetidae when proposing his subdivision. Until this point is clarified, I prefer to leave open the question of how the Drosophiloidea should be divided into prefamilies. My delimitation of the families of Drosophiloidea (see table 2) follows that customary in recent literature, except that my transference of *Diastata* to the Ephydriidae requires the new name Campichoetidae to be proposed for the residue of the former "Diastatidae". Some of the characters on which the family classification is based are indicated on figure 15.

Superfamily Nothyboidea

Hennig (1958) tentatively proposed a group Nothyboidea, in which he included the Megamerinidae, Nothybidae, Diopsidae, Psilidae, Tanypezidae and Strongylophthalmyiidae. It is apparent from my studies that this group is heterogenous. In this paper I refer the Megamerinidae, Diopsidae and Tanypezidae (including Strongylophthalmyiidae) to different prefamilies of Muscoidea (the Sciomyzoinea, Diopsioinea and Tanypezoinea respectively). In my revised sense of Nothyboidea I include the Nothybidae, Psilidae, Teratomyzidae and Periscelididae (including *Somatia*).

My conclusion that the Nothyboidea in my revised sense is probably monophyletic, is based on the following groundplan conditions which are apomorphous with respect to the groundplan of the Schizophora:

- (1) Aedeagus (♂) articulated with aedeagal apodeme, swung through wide arc from anteriorly directed rest position to copulatory position, with basal phallophore and variable differentiation of distal sclerotization in its walls.

I ascribe to the groundplan of the Nothyboidea and Muscoidea the presence of a well developed mechanism for swinging the aedeagus through a wide arc against the aedeagal apodeme (see further below in my discussion of Muscoidea). The common presence of this mechanism can probably be ascribed to synapomorphy. Such a mechanism is always lacking in the Lonchaeoidea, Lauxanioidea and Drosophiloidea. The swinging mechanism is well developed in three families of Nothyboidea, the Nothybidae, Teratomyzidae and Psilidae. The other family, Periscelididae, shows a type of aedeagus which I interpret as highly apomorphous and not indicative of the groundplan of the superfamily. I am not able to suggest the precise condition of the aedeagus in the groundplan of the Nothyboidea beyond the presence of the swinging mechanism. The types of aedeagus shown by the Nothybidae, Teratomyzidae and Psilidae are divergent and possibly all apomorphous to some degree. In Nothybidae part of the aedeagus is flexible and ribbon-like, comparable with the condition of Periscelididae (in which the aedeagus is flexible and ribbon-like along most of its length). But the presence of a flexible area of the aedeagus is probably not a groundplan condition of the Nothyboidea, as the aedeagus of Teratomyzidae is rigid throughout (as I postulate also for the groundplan of the Muscoidea).

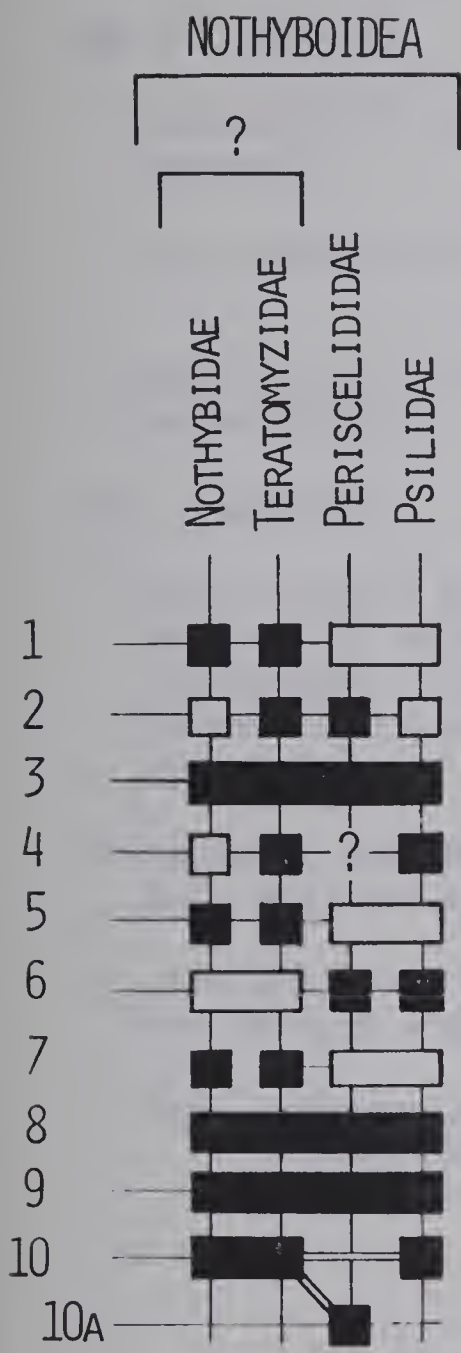


Fig. 16. Distribution of some character states among the families of Nothyboidea. The black rectangles indicate groundplan conditions interpreted as apomorphous with respect to the groundplan of the Schizophora. Where common possession of such apomorphous conditions is interpreted as due to synapomorphy, a continuous black rectangle is shown against the families concerned. Corresponding plesiomorphous conditions are shown by the white rectangles. The condition indicated at 10a is considered to be a further modification of that at 10. Some autapomorphous conditions of single families have been omitted. The list of characters is as follows.

Apomorphous conditions
(black rectangles)

Plesiomorphous conditions
(white rectangles)

Head

- | | |
|------------------------------|---------------------------------|
| 1. Postverticals reduced | Divergent postverticals present |
| 2. Only 1 <i>ors</i> present | 2 <i>ors</i> present |

Thorax

3. Only 1 *pa* present

Wing

- | | |
|---|----------------------------------|
| 4. Subcosta not reaching wing margin as distinct vein | Subcosta distinct to wing margin |
|---|----------------------------------|

(Cont'd)

Fig. 16 (Cont'd)

- | | |
|---|--|
| 5. Axillary lobe and alula reduced | Axillary lobe and alula normal |
| 6. Anal vein cut off apically | Anal vein long, almost or fully reaching wing margin |
| 7. Lower basal cell open anterodistally | Lower basal cell fully closed |

Male postabdomen

- 8. Only a single dorsal sclerite between 6th segment and hypopygium; no ventral sclerites between 6th sternum and hypopygium
- 9. Aedeagal apodeme fused with body wall posteriorly
- 10. Aedeagus swung through wide arc against aedeagal apodeme
 - 10a. Aedeagus ribbon-like, without swinging mechanism

- (2) Only one dorsal sclerite between 6th segment and hypopygium (♂); no ventral sclerites between 6th sternum and hypopygium (figs. 43, 46 and 51).

The homology of this dorsal pregenital sclerite requires clarification. Two interpretations seem possible. If it is postulated that the postabdominal morphology of the Nothyboidea is derived from the condition ascribed to the groundplan of the Muscoidea (see below), then the dorsal sclerite preceding the hypopygium may be interpreted as the fused 7th and 8th sterna. But this interpretation is problematical because in most Nothyboidea this sclerite is symmetrical, and I have not found any trace of a suture line indicating that fusion of separate areas of sclerotization has occurred. It is true that in *Somatia* (Periscelididae) this sclerite is asymmetrical, more strongly developed on the left side; but this asymmetry is probably secondary, not ascribable to the groundplan of the Nothyboidea or Periscelididae, since the structure of the abdomen in *Somatia* is highly modified in many respects. In all Nothyboidea except *Somatia* the dorsal pregenital sclerite is symmetrical. An alternative interpretation must therefore be considered, namely that the dorsal pregenital sclerite represents an unreduced 7th tergum. The position of the 7th spiracles in Nothyboidea conforms well with this interpretation, since these are always situated (when present) below or within the dorsal pregenital sclerite. If this latter interpretation is correct, then the postabdominal structure of the Nothyboidea cannot be derived from the condition shown in the groundplan of the Muscoidea, in which the sclerites of the 7th segment have been asymmetrically reduced. The homology of the dorsal pregenital sclerite is thus of crucial importance for the classification here proposed. My recognition of the Nothyboidea as a full superfamily rests on the postulate that the second explanation (that the Nothyboidea show an unreduced 7th tergum) is more probably correct. If, to the contrary, it can be shown that the postabdominal structure of the Nothyboidea is in fact derived from the condition shown in the groundplan of the Muscoidea, then the Nothyboidea should be reclassified as a prefamily of Muscoidea.

In all species which I have studied the last ventral sclerite before the hypopygium is the 6th sternum, which is symmetrical and, except in Nothybidae, of similar size to the preceding sterna. Verbeke (1952) reports that in some *Loxocera* species (Psilidae) an additional narrow band of ventral sclerotization is present, which he interprets as the 7th sternum. If the presence of a symmetrical 7th sternum can be ascribed to the groundplan of the Nothyboidea, then the view that the condition of the postabdomen in Nothyboidea has not been derived from the condition shown in the groundplan of the Muscoidea will be strengthened, because the 7th sternum is asymmetrically developed in the groundplan of the Muscoidea (becoming fused with the inverted 8th sternum on the left side). However, since this apparent 7th sternum has so far only been reported in a few species of a single genus, it is possible that it represents a secondary sclerotization. The characterization given above is based on the postulate that the last ventral sclerite present in the groundplan of the Nothyboidea was an unmodified 6th sternum.

Clearly the considerations presented here have not definitely settled the question of what modifications of the 7th and 8th abdominal segments occurred in the groundplan of the Nothyboidea. Relevant information from ontogenetic studies or studies of intersexes would be of great interest. In view of the doubt about the homology of the last dorsal sclerite before the hypopygium, I refer to this as the "pregenital sclerite" in this work.

(3) Aedeagal apodeme (σ) fused with body wall posteriorly.

In Nothybidae, Teratomyzidae and some Psilidae the aedeagal apodeme is fused with the body wall posteriorly (between the hypandrial arms), as far as its ventral spur (figs. 44 and 50); only the anterior end of the apodeme remains free in the body cavity. This condition seems more plesiomorphous than the complete fusion of the apodeme with the body wall shown by most Periscelididae and some groups of Psilidae. Only in *Somatia* (Periscelididae) is the aedeagal apodeme free from the body wall along its entire length; this condition is probably secondary, associated with reduction of the hypandrium.

(4) Only one postalar bristle (*pa*) present.

Hennig (1965b, 1969a, in press) reports this as an apomorphous condition of the Nothybidae, Teratomyzidae, Periscelididae and Psilidae.

The Nothyboidea retain (at least in their groundplan) many plesiomorphous conditions. These include an unmodified 6th segment in the male, a complete subcosta, the absence of vibrissae, and an apparently unmodified female postabdomen (as shown by *Nothybus*; see Hennig 1958, fig. 78).

Whether the costa was broken or unbroken in the groundplan of the Nothyboidea is not clear. The costa is unbroken in Nothybidae and Periscelidinae, but broken in Psilidae, Teratomyzidae and *Somatia* (Periscelididae).

I do not propose a division of the Nothyboidea into prefamilies at present, since I am in doubt as to which families are most closely related to one another. The Periscelididae and Teratomyzidae share certain apomorphous conditions of the head. However, certain modifications in the structure of the wing are shown by the Teratomyzidae and Nothybidae, but not by the Periscelididae. The Psilidae are highly modified in some respects, and it is difficult to judge whether they are the sister-group of all other

Nothyboidea or most closely related to one of the other families. Some of the characters on which the family classification is based are indicated on figure 16.

Hennig (in press) classifies the Periscelididae and Teratomyzidae along with the Aulacigastridae and Asteiidae in a subgroup (Periscelidea) of the Anthomyzoinea. In my opinion the "Periscelidea" are polyphyletic, or at least diphyletic. The Aulacigastridae and Asteiidae show the typical muscoid structure of the male postabdomen, and I accept their classification in the Anthomyzoinea (Anthomyzoidea of Hennig). But the structure of the male postabdomen in Periscelididae and Teratomyzidae is fundamentally different, and seems to me incompatible with their classification in the Anthomyzoinea. Since the apomorphous conditions on which Hennig's proposal is based (large peristomal opening; 2 *ors* in groundplan; only 1 *pa*) are all rather widely distributed, I think that his proposal should be rejected on grounds of incompatibility with the distribution of the additional characters which I treat in this work.

Superfamily Muscoidea

The name Muscoidea has been used in a variety of senses. It has often been used for the whole of the Schizophora, corresponding with Coquillett's (1901) original proposal except that he excluded the Pupipara (Hippoboscidae s.l.). However the use of the name in this wide sense is superfluous, since the well-known name Schizophora has priority. Recent authors have generally applied the superfamily category to subordinate groups of the Schizophora, and I think it preferable to follow this tradition, at least until sufficient information is available for applying the time criterion of ranking. Some recent authors have restricted the name Muscoidea to part

Caption for Fig. 17.

Fig. 17. Distribution of some character states among the families of Muscoidea. This figure is intended to summarize the distribution of conditions shown by a range of families. All entries refer to the postulated groundplan condition for each family. Various autapomorphous conditions of single families or family-groups have been omitted: many characters of the female postabdomen have also been omitted because comprehensive information on them is not available. The black rectangles indicate conditions interpreted as apomorphous with respect to the groundplan of the Schizophora. Where common possession of such apomorphous conditions is interpreted as due to synapomorphy, a continuous black rectangle is shown against the families concerned. Corresponding plesiomorphous conditions are shown by the white rectangles. Further modifications of a primary apomorphous condition are shown in separate rows, with synapomorphy at the primary level indicated by linking the rectangles. The list of characters is as follows.

Apomorphous conditions
(black rectangles)

Plesiomorphous conditions
(white rectangles)

Head

1. 2nd antennal article with cleft	2nd antennal article without cleft
2. Ocellar bristles reduced	Ocellar bristles well developed
3. <i>Ori</i> present	<i>Ori</i> absent
4. Only 1 <i>ors</i> present	At least 2 <i>ors</i> present
4a. <i>Ors</i> absent	
5. 1 or no <i>vt</i> present	2 <i>vt</i> present
6. <i>Pvt</i> parallel or convergent	Divergent <i>pvt</i> present
7. <i>Pvt</i> reduced or absent	(as 6)
8. External mouth opening with prestomal teeth	Prestomal teeth absent
9. Hyoid present	Hyoid absent
10. Pseudotracheae opening into one or two main channels	Pseudotracheae opening directly into external mouth opening

(Cont'd)

Fig. 17 (Cont'd)

Wing

- | | |
|---|--------------------------------------|
| 11. Costa broken at end of sc
or r ₁ | Costa unbroken |
| 11a. Costa broken twice | |
| 11b. Costa broken near humeral
cross-vein | |
| 11c. Costa secondarily
unbroken | |
| 12. Subcosta faded or fused with
r ₁ distally, not reaching wing
margin as distinct vein | Subcosta distinct to wing
margin |
| 13. Anal vein not reaching wing
margin as a distinct vein | Anal vein distinct to wing
margin |
| 13a. Anal vein and anal cell
lost | |
| 14. Lower cross-vein lost | Lower cross-vein present |

Preabdomen

- | | |
|--|-------------------------------------|
| 15. 2nd to 5th spiracles within
terga | 2nd to 5th spiracles in
membrane |
| 15a. 3rd to 5th spiracles
secondarily in membrane | |

Male postabdomen

- | | |
|---|-------------------------------------|
| 16. 6th tergum shorter than 5th
tergum | 6th tergum as long as 5th
tergum |
| 16a. 6th tergum asymmetrically
reduced | |
| 16b. 6th tergum reduced to two
fragments | |
| 16c. 6th tergum lost | |
| 16d. 6th tergum fused with
8th sternum | |

(Cont'd)

Fig. 17 (Cont'd)

- 17. 6th sternum more strongly developed on left side
 - 17a. 6th sternum secondarily symmetrical
 - 17b. 6th sternum triangular
 - 17c. 6th sternum linked to pregenital sclerite on both sides, or forming part of this sclerite
 - 17d. 6th sternum reduced or lost
- 18. 7th sternum asymmetrical, extending dorsally on left side
 - 18a. 7th sternum forming complete ventral band
 - 18b. 7th sternum not delimited, absent or fully fused with 8th sternum to form a composite pregenital sclerite
 - 18c. Pregenital sclerite divided into lateral plates
- 19. 8th sternum or pregenital sclerite reduced to narrow band
 - 8th sternum (or pregenital sclerite) large
- 20. 7th tergum reduced to latero-ventral vestige
 - 20a. 7th tergum vestige lost
- 21. 8th tergum vestige lost
 - 8th tergum vestige present
- 22. 7th spiracles lost (both sides)
 - 6th and 7th spiracles present in membrane on both sides
- 23. 6th and 7th spiracles lost (both sides)
 - (as 22)

(Cont'd)

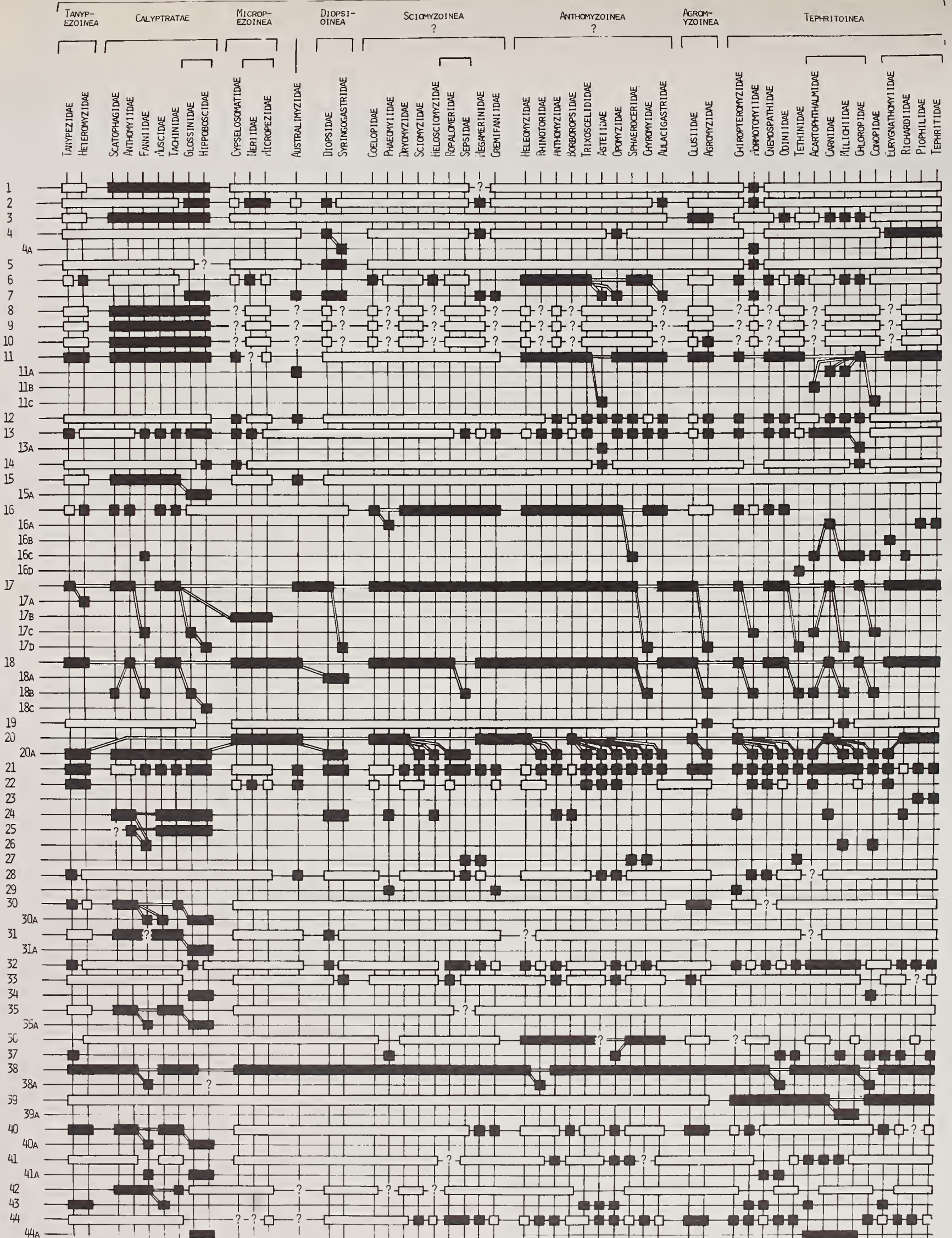
Fig. 17 (Cont'd)

- | | |
|---|--|
| 24. 7th left spiracle within
7th sternum | (as 22) |
| 25. 7th right spiracle within
8th sternum | (as 22) |
| 26. 6th and 7th spiracles on both
sides within pregenital
sclerite | (as 22) |
| 27. various other modifications
in position and/or numbers
of postabdominal spiracles | (as 22) |
| 28. Telomeres lost or fused with
periandrium | Telomeres discrete, not double
or bifid |
| 29. Telomeres double or bifid | (as 28) |
| 30. Processus longi well
differentiated | Processus longi poorly
differentiated or absent |
| 30a. Processus longi
secondarily lost | |
| 31. Cerci linked to telomeres | Cerci not linked to telomeres |
| 31a. Cerci reduced (not
linked to telomeres) | |
| 32. Aedeagal apodeme linked or
fused with the hypandrium
or the area between the
hypandrial arms | Aedeagal apodeme free from body
wall |
| 33. Hypandrial arms fused above
base of aedeagus | Hypandrial arms not fused, nor
forming a trough |
| 34. Hypandrial arms forming a
trough or sheath around
aedeagal apodeme and base
of aedeagus | (as 33) |
| 35. Articulated pregonites
present | Pregonites absent or not
articulated |

(Cont'd)

Fig. 17 (Cont'd)

- | | |
|--|------------------------------------|
| 35a. Pregonites secondarily reduced | |
| 36. Postgonites setose | Bare postgonites present |
| 37. Postgonites reduced | (as 36) |
| 38. Base of aedeagus swung through a wide arc against aedeagal apodeme | |
| 38a. Aedeagus directed postero-ventrally at rest (swinging mechanism secondarily lost) | |
| 39. Aedeagus long and flexible, coiled when at rest | Aedeagus not of this type |
| 39a. Aedeagus reduced | |
| 40. Epiphallus present | Epiphallus absent |
| 40a. Epiphallus secondarily lost | |
| 41. Ejaculatory apodeme reduced | Ejaculatory apodeme well developed |
| 41a. Ejaculatory apodeme lost | |
| <i>Female postabdomen</i> | |
| 42. 7th spiracles displaced anteriorly | 7th spiracles on 7th segment |
| 43. 7th spiracles lost | (as 42) |
| 44. 2 spermathecae | 3 spermathecae |
| 44a. Spermathecae reduced | |



of the Calyptratae, following Roback (1951). However, Roback's proposed group is probably not monophyletic (see my comments below on the Calyptratae), and I am reluctant to use the superfamily category at such a low level in the sequence of subordination because of the proliferation of superfamily names in other parts of the classification which this would entail. Accordingly I apply the superfamily category in this paper at a much higher level than Roback has proposed, but at a lower level than Coquillett. My concept of Muscoidea is substantially new, based on characters of the male postabdomen and genitalia which have not previously been analysed in sufficient detail to be used for classification. Although no previous authors have proposed a group corresponding to the whole of the Muscoidea in my sense, the relationships between many of the included families have been recognized. For instance, Hendel's (1936) groups Trypetides and Sciomyzides consisted largely of series of muscoid families, although a few heterogenous families were also included. Hennig (1958) made considerable progress towards defining some of the major subordinate groups of Muscoidea, but the possibility of delimiting a wider group of the kind now proposed was not indicated by the characters considered in his analysis.

I consider the Muscoidea in my sense to be monophyletic on the basis of the following conditions of their groundplan which are apomorphous with respect to the groundplan of the Schizophora:

- (1) 7th abdominal sternum (σ) strongly asymmetrical, extending dorsally on left side until becoming fused or contiguous at its dorsal extremity with inverted 8th sternum.

This characteristic condition of the 7th sternum can be readily recognized in most Muscoidea, except for a few groups in which the sclerotization of the postabdomen has been reduced or simplified. Because the 7th sternum extends dorsally on the left side, some authors have maintained that this

sclerite represents the 7th tergum. But this view is not reconcilable with its position between the spiracles of the segment; and the sternal nature of the sclerite is further shown by its frequent retention of the *sensilla trichodea* (which form a homonomous series as far as the 7th sternum in the groundplan of the Cyclorrhapha). I have noted such sensilla on the 7th sternum of Muscoidea in members of the Tanypezidae and Heteromyzidae (Tanypezoinea), Dryomyzidae (fig. 89) (Sciomyzoinea), Heleomyzidae (fig. 101) (Anthomyzoinea), Clusiidae (Agromyzoinea), and Tephritidae s.l. and Odiniidae (Tephritoinea). This list is probably not exhaustive, as the sensilla may be present in members of other families but be too small to be resolved with a binocular microscope. From the above considerations I think that the homology of the 7th sternum in Muscoidea is clear beyond reasonable doubt.

- (2) 7th tergum (♂) asymmetrically reduced to small vestige situated lateroventrally on right side; 7th right spiracle displaced towards centre-line.

The vestige of the 7th tergum has sometimes been overlooked, as it is usually infolded between membrane and often cannot be detected unless the abdomen has been macerated and extended. According to my observations this tergum vestige is present as a discrete sclerite in members of the following families: Micropezidae (fig. 71), Neriidae and Cypselosomatidae (Micropezoinea), Coelopidae (fig. 81), Phaeomyiidae (fig. 85), Dryomyzidae, Megamerinidae (fig. 77) and Cremifaniidae (fig. 99) (Sciomyzoinea), Heleomyzidae (fig. 101) and Borboropsidae (fig. 111) (Anthomyzoinea), Clusiidae (fig. 119) (Agromyzoinea), and Chiropteromyzidae (fig. 122), Carnidae (fig. 134), Piophilidae s.l., Tephritidae s.l. and Richardiidae (fig. 142) (Tephritoinea). This wide distribution convinces me that such a vestigial sclerite should be ascribed to the groundplan of the Muscoidea. I interpret the vestige as representing the right lateral extremity of the 7th tergum, which has been asymmetrically reduced. It cannot be derived from the sternum, since it always lies to the right of the 7th right spiracle.

In those Muscoidea in which the 7th tergum vestige is retained, the adjacent 7th right spiracle is usually displaced towards the centre-line in relation to the preceding spiracles.

- (3) 6th sternum (♂) asymmetrical, more strongly developed on left side where it extends towards 7th sternum.

The 6th sternum is asymmetrical in nearly all Muscoidea, except those in which it has been modified through fusion with the 7th and 8th sterna. Only in the Heteromyzidae (Tanypezoinea) does a large symmetrical discrete 6th sternum occur, similar to the sterna of the preceding segments. However, since members of the Tanypezidae, which I include with the Heteromyzidae in the Tanypezoinea, show an asymmetrical 6th sternum, I think it possible that the apparently unmodified condition of the 6th sternum shown by the Heteromyzidae is secondary (apomorphic). Accordingly, I postulate that asymmetrical development of the 6th sternum can be ascribed to the

groundplan of the Muscoidea. I think that a symmetrical 6th sternum should be ascribed to the groundplan of all other superfamilies of Schizophora.

- (4) Hypandrium (♂) linked to anterior margin of inverted 8th sternum by unpaired muscle on left side (*musculus hypandriotergalis* of Salzer 1968).

This muscle has been called the *musculus hypandriotergalis* (M 33) by Salzer (1968). I use Salzer's term in this work, although it is not wholly appropriate because it implies that the inverted 8th sternum is a tergum. Other names which have been applied to this muscle are *M. introtractor longus anterior* (Schröder 1927), M 8 (Hennig 1936a), and muscle "j" (Gooding and Weintraub 1960). Salzer states that it is the only unpaired muscle in the postabdomen of *Calliphora* which does not show indications of paired origin. Since I can find no such muscle in the Syrphidae or Platypezidae (the most relevant non-schizophorous families of Cyclorrhapha because of their retention of a large 8th sternum), I am convinced that its presence in many Muscoidea is apomorphous. No homologous muscle has been reported in members of any other superfamily of Schizophora. The list of the groups of Muscoidea for which the presence of this muscle has been reported in the literature is as follows: Micropezidae (*Calycopteryx*, Hennig 1936a), Tachinidae s.l. (*Ernestia*, Petzold 1927; *Calliphora*, Schröder 1927 and Salzer 1968; *Hypoderma*, Gooding and Weintraub 1960). On the basis of serial sections which I have made, I can add *Pherbellia* (Sciomyzidae), *Nemopoda* (Sepsidae), *Clusia* (Clusiidae), *Anthomyza* (Anthomyzidae) and *Leptocera* (Sphaeroceridae). Only for the Tephritoinea is there definite information that this muscle is absent (see my comments on that prefamily below). Since the presence of the *musculus hypandriotergalis* has now been confirmed for five prefamilies of Muscoidea, I postulate that this muscle was present in the groundplan of the Muscoidea and has been secondarily lost in the Tephritoinea. Of course, information on members of additional groups is needed to test the validity of this hypothesis.

- (5) Aedeagus (♂) articulated with aedeagal apodeme, swung through wide arc from anteriorly directed rest position (fig. 52) to copulatory position (fig. 53), with basal phallophore and at least a pair of lateral sclerites (paraphalli) differentiated in its walls.

It is clear that the Muscoidea are characterized in their groundplan by a large aedeagus which is directed anteriorly (folded into a genital pouch beneath the hypandrium and aedeagal apodeme) in the rest position, but swung out posteriorly through a wide arc for copulation. The copulatory position corresponds with the position of the aedeagus in Lonchaeoidea, Drosophiloidea, Lauxanioidea and non-schizophorous Diptera, in which no swinging mechanism has developed. Salzer (1968: 204-206) has recently described in detail the mechanisms involved in extruding and retracting the aedeagus of *Calliphora erythrocephala* Meigen, a species in which a strong swinging action is shown. His figures (reproduced as my figs. 52 and 53)

indicate movement of the aedeagus through an angle of about 160° about its articulation with the aedeagal apodeme. In the groundplan of the Muscoidea the aedeagus was probably a rigid structure whose extrusion was achieved primarily by muscular action; probably the only well-defined sclerites were a basal ring or partial ring on which muscles insert (the phallopore), with which were joined a pair of elongate sclerites (paraphalli) strengthening the walls of the aedeagus. The varied types of aedeagus found in different muscoid families can all be interpreted as further developments from such a basic type. Additional distal sclerites of the aedeagus are differentiated in many groups of Muscoidea, but the development of such sclerites is very variable, even between closely related groups. Whether the presence of such distal sclerites can be ascribed to the groundplan of the Muscoidea seems to me doubtful, since they are not differentiated, for instance, in the Tanypezoinea. The development of this characteristic mechanism for swinging the base of the aedeagus through a wide arc against the aedeagal apodeme by means of muscles inserted on the phallopore, probably constitutes a synapomorphy between the Muscoidea and Nothyboidea. This mechanism is lacking in the Lonchaeoidea, Lauxanioidea and Drosophiloidea, in which the aedeagus remains in the same direction relative to the aedeagal apodeme when at rest.

My use of the term paraphalli for the pair of lateral sclerites in the walls of the aedeagus follows the practice of authors on Calyptratae. The term was originally proposed in the singular ("paraphallus") by Lowne (1893), since in *Calliphora* (Tachinidae s.l.) these sclerites are fused basally where they join the phallopore. Wesché (1906) amended this usage to the plural paraphalli.

The Muscoidea exhibit in their groundplan some significant plesiomorphous conditions in comparison with other superfamilies of Schizophora. Most noteworthy is the condition of the inverted 8th abdominal segment (σ), which is clearly defined and retains a large dorsal sternum and a small ventral vestige of the 8th tergum (as also in Platypezidae). The 8th tergum vestige is frequently lost, but its retention in the groundplan of the Muscoidea is indicated by its presence as a distinct sclerite in members of the Scatophagidae and Anthomyiidae (fig. 61) (Calyptratae), Cypselosomatidae (fig. 71), Neriidae and Micropezidae (Micropezoinea), Coelopidae (fig. 81) and Phaeomyiidae (fig. 85) (Sciomyzoinea), Heleomyzidae (fig. 101) (Anthomyzoinea) and Richardiidae (fig. 142) (Tephritoinea). The only group of Schizophora apart from the Muscoidea in which the 8th

tergum vestige is retained is the Lonchaeidae (Lonchaeoidea). Another plesiomorphous condition of the male abdomen in the groundplan of the Muscoidea is the retention of an unmodified 6th tergum, fully as long as the preceding 5th tergum. This condition is well shown, for instance, by the Micropezoinea (fig. 72), Australimyzoinea (fig. 74) and many Agromyzoinea (fig. 120). In respect of the characters of the chaetotaxy, wing venation and female postabdomen analysed by Hennig (1958), the Muscoidea include groups which show both plesiomorphous and apomorphous conditions. These characters do not aid in the definition of the Muscoidea, at least on the basis of existing analyses, but only in its further subdivision.

Within some subordinate groups of Muscoidea there is a strong tendency for the structure of the postabdomen to become simplified through loss of the 7th and 8th tergum vestiges and fusion of the 7th and 8th sterna. Such changes have occurred independently in many families. Nevertheless, I wish to emphasize that all the highly modified conditions of the male postabdomen shown by particular groups here included in the Muscoidea are, in my opinion, secondarily derived from the condition ascribed to the groundplan of the Muscoidea. I have not included in the Muscoidea any group with symmetrical male postabdomen for which there is no clear evidence that this condition is secondary because other characters indicate a close relationship to groups showing the characteristic muscoid structure. My conclusion that the Muscoidea are monophyletic is based not on any vague distinction between asymmetrical and symmetrical types of postabdomen, but on a particular and precisely definable asymmetrical condition of their groundplan, as indicated in my characterization above. Asymmetrical conditions of some of the postabdominal sclerites are also

shown by a few members of other superfamilies, notably *Eurychoromyia* (Lauxanioidea) and *Somatia* (Periscelididae, Nothyboidea), but these conditions appear to be derived from symmetrical conditions in the groundplan of those superfamilies. It is possible that the male postabdomen was also asymmetrical (but probably only weakly so) in the groundplan of the Lonchaeoidea, as previously discussed. The male postabdomen was probably fully symmetrical in the groundplan of the remaining superfamilies of Schizophora (Lauxanioidea, Drosophiloidea and Nothyboidea).

I have found the subdivision of the Muscoidea into subordinate groups problematical, because of the basic similarity in the structure of the male postabdomen and genitalia in the groundplan of many families. Further analyses of other organ systems are desirable in order to improve the classification. The groups Sciomyzoinea and Anthomyzoinea are particularly in need of critical study, since they are based on weak characterization. The possibility that these groups may be paraphyletic because they include families more closely related to one of the other prefamilies, should be borne in mind in future studies. The other groups here recognized as prefamilies (Tanypezoinea, Calyptratae, Micropezoinea, Australimyzoinea, Diopsioinea, Agromyzoinea and Tephritoinea) seem to me to represent probable monophyletic groups on the basis of the characterization given below. Some of the characters on which the family classification is based are indicated on fig. 17.

Prefamily Tanypezoinea

In this group I include two families, the Tanypezidae (including *Strongylophthalmyia*) and the Heteromyzidae. This grouping is new, although perhaps anticipated by Brauer's (1880) reference of both families to the

"Schizometopa". The agreement in apomorphic conditions between these two families is substantial, and I see no good reason to ascribe it to homoplasy. I characterize the Tanypezoinea by the following groundplan conditions which are apomorphic with respect to the groundplan of the Muscoidea:

- (1) 7th abdominal spiracles lost in both sexes.

Loss of spiracles occurs in only a few groups of Muscoidea, notably in certain Anthomyzoinea and Tephritoinea, and such reduction has not always proceeded in parallel in both sexes. Other families in which parallel loss of the 7th spiracles has occurred in both sexes are the Trixoscelididae, Opomyzidae and Asteiidae (Anthomyzoinea) and the Eurygnathomyiidae, Mormotomyiidae and Cnemospathidae (Tephritoinea). Doubtless these other cases are due to homoplasy with the condition shown by the Tanypezoinea, as the other characters of the groups concerned do not suggest that they are most closely related to the Tanypezoinea. Probably the loss of the 7th spiracles in Tanypezoinea is an autapomorphic condition.

- (2) 7th and 8th abdominal segments (♀) elongate, forming slender ovipositor which can be retracted within 5th and 6th segments (see Hennig 1958, figs. 79, 84 and 242).
- (3) 7th and 8th tergum vestiges lost (♂).
- (4) Sclerotized fold (epiphallus) projecting posteriorly from base of aedeagus (♂) (figs. 54 and 58).
- (5) Costa broken at end of subcosta (see Hennig 1958).

The above apomorphic conditions are combined with certain noteworthy plesiomorphic conditions. The 6th segment of the male abdomen is little modified, bearing a large tergum and sternum (figs. 55 and 56). In Tanypezidae the 6th sternum is distinctly asymmetrical, more strongly developed on the left side, while in Heteromyzidae it appears almost symmetrical. It is not clear which condition should be ascribed to the groundplan of the Tanypezoinea. If the large, almost symmetrical 6th sternum shown by the Heteromyzidae corresponds to the groundplan condition of the

Tanypezoinea, then this is the only prefamily of Muscoidea showing an almost symmetrical 6th sternum in its groundplan (apart from groups showing conditions which are obviously secondary). However, if the 6th sternum was large and almost symmetrical in the groundplan of the Muscoidea, it is puzzling that such a condition has not been retained by any group other than the Heteromyzidae. I think it more parsimonious, at least on present information, to postulate that the distinctly asymmetrical condition of the 6th sternum shown by the Tanypezidae corresponds to the groundplan condition for the Tanypezoinea and for the Muscoidea as a whole (as indicated in my characterization of the Muscoidea above).

Another noteworthy condition of the Tanypezoinea which is probably plesiomorphous for the Muscoidea, is sexual dimorphism in the size of the eyes (resulting in a narrower frons in the male). I consider such a condition to be plesiomorphous for the Schizophora, as indicated above in my discussion of the Lonchaeoidea. To my knowledge the only groups of Muscoidea which show a pronounced sexual dimorphism of this kind are the Calyptratae and Tanypezoinea, apart from the almost certainly secondary case of *Neomaorina* (Tephritidae family-group). The dimorphism is shown by many members of both families of Tanypezoinea, although lost in a few groups (such as *Strongylophthalymia*).

The aedeagi of the northern hemisphere genera of Tanypezidae may at first sight seem very different from those of the Heteromyzidae. But the morphological gap is bridged by the neotropical *Neotanypeza* (fig. 54), which has a rather short aedeagus whose sclerotization includes a pair of lateral paraphalli and a weakly sclerotized semicylindrical area (probably part of the wall of the ejaculatory duct) lying between the paraphalli. This condition of the aedeagus distinctly resembles the condition shown by

the Heteromyzidae (fig. 58), in which the ejaculatory duct is conspicuously sclerotized. However, it is not clear whether the Tanypezoinea can be characterized as apomorphous in their groundplan in respect of sclerotization of the ejaculatory duct, as such sclerotization is scarcely developed in *Tanypeza* and *Strongylophthalmyia*.

The Tanypezidae have divergent postvertical bristles, while in the Heteromyzidae these are convergent. Which condition should be ascribed to the groundplan of the Tanypezoinea is not clear. The same doubt applies to the development of oral vibrissae, which are more or less differentiated in the Heteromyzidae but not in the Tanypezidae.

Aczél (1951) placed the Tanypezidae with the Micropezoinea in a group "Tanypezidiformes", but I am unable to find firm grounds for supposing that the Tanypezidae (or the Tanypezoinea as a whole) are more closely related to the Micropezoinea than to other Muscoidea. Aczél did not give a convincing definition of the "Tanypezidiformes" in terms of synapomorphous conditions, and I therefore support Hennig (1958) in rejecting his proposal.

Prefamily Calyptratae

(= Thecostomata Frey)

The name *Schizometopa* Brauer is often listed as an additional synonym of the Calyptratae, but these groups only partly coincide since Brauer (1883) included the Tanypezoinea in the *Schizometopa* but excluded the Scatophagidae.

The Calyptratae are one of the most surely grounded monophyletic groups within the Schizophora. The definition of the group has been studied by many workers, with the result that a long list of conditions can now be

put forward as probable groundplan conditions of the Calyptratae which are apomorphous with respect to the groundplan of the Muscoidea:

- (1) 2nd antennal article with longitudinal cleft or suture externally.

This condition is by no means confined to the Calyptratae (as implied in some identification keys), but also occurs widely among the Lonchaeidae and Drosophiloidea, and in some genera of Tephritoidea, Megamerinidae and Psilidae. However there seem to be no sufficient grounds for considering any of these groups most closely related to the Calyptratae, and I therefore think that the presence of this suture is probably an autapomorphous condition of the Calyptratae, in agreement with Hennig (1958). Hennig (in press) gives important new information and discussion on the structure of the antennae in Schizophora.

- (2) Lower fronto-orbital bristles (*ori*) present (Hennig 1958).
- (3) Anterior upper fronto-orbital (*ors*) proclinate (Hennig 1958).
- (4) Vibrissae present (Hennig 1958).
- (5) Posthumeral or intra-alar bristles (or both) present (Girschner 1893, 1896).

It is probable that the presence of one or other of these bristles may be ascribed to the groundplan of the Calyptratae, but the sequence of conditions involved has not been clarified.

- (6) Costa broken at end of subcosta.

Hennig (1965a: 5) now accepts this as a groundplan condition of the Calyptratae, contrary to his earlier view (Hennig 1958: 678).

- (7) Abdominal spiracles 2-5 (♂) or 2-6 (♀) lying within side-margins of respective terga.

It is arguable that this condition does not belong to the groundplan of the Calyptratae, if the Hippoboscidae family-group is the sister-group of all other Calyptratae (see below). However, even if this hypothesis is correct, I am doubtful whether the characterization given above should be revised. I think that the situation of (at least) the 3rd to 5th spiracles in membrane in members of the Hippoboscidae family-group may well be secondary, resulting from expansion of the area of abdominal membrane to allow greater distension when a blood meal is obtained. I draw a distinction between the sexes in respect of this character, since the 6th spiracles lie in membrane in most male Calyptratae and there is no reason to doubt that this was also so in the groundplan of the group.

- (8) 7th left spiracle (♂) lying within 7th sternum, displaced dorsally in relation to spiracles of preceding segments (figs. 59, 61 and 67).

In the groundplan of the Muscoidea the 7th left spiracle lay in membrane before the 7th sternum. Its inclusion within the 7th sternum in Calyptratae is apomorphous. A similar modification has occurred sporadically among other groups of Muscoidea, but is much less widespread than the situation of this spiracle in membrane.

- (9) 7th tergum vestige lost (♂).

I found no trace of the 7th tergum in any Calyptratae. But I noted the presence of the 8th tergum vestige in *Cordilura* (Scatophagidae) and *Pegomya* (fig. 61) (Anthomyiidae).

- (10) Large articulated pregonites present (♂) (figs. 60 and 70).

The pregonites of Calyptratae are a second pair of paraphyses according to my interpretation of Black's (1966) observations (see section 3.1 above). Although pregonites (or analogous structures) are present in many groups of Schizophora, I do not know of any group other than the Calyptratae in which they are fully articulated. According to Salzer (1968) muscles originating from the aedeagal apodeme (M 38, *musculi phallapodemoparamerales anteriores*) are inserted on the base of the pregonites ("Proparameren").

- (11) Epiphallus (♂) well developed (figs. 60, 62, 65 and 70).

A long epiphallus (posterior process of the phallophore) should probably be ascribed to the groundplan of the Calyptratae. Such a structure is widely distributed among all families except the Fanniidae and the Hippoboscidae family-group.

- (12) Processus longi present (fig. 70).

The processus longi are paired sclerites articulated at either end with the vertical sections of the hypandrial arms and the outer basal processes of the telomeres. They are absent in the Hippoboscidae family-group, Muscidae and Fanniidae, but present in Tachinidae (s.l.), Anthomyiidae and Scatophagidae. This distribution suggests that such sclerites were probably present in the groundplan of the Calyptratae.

Frey (1921: 208) interpreted three conditions of the mouthparts as "specializations" of the Calyptratae, as follows:

- (13) External mouth-opening with prestomal teeth;
(14) Inner mouth-opening with hyoid (= theca, Gelenkkapsel); and

- (15) Pseudotracheae with both dorsal and ventral main channel ("Sammlungsrohr").

Since Frey studied members of seven genera of Scatophagidae, I regard the absence of character 15 in the scatophagid *Pogonota* reported by van Emden (1950) as secondary. The hyoid is secondarily lost in Stomoxyinae (Muscidae) and some Hippoboscidae.

The Calyptratae as here defined include the Pupipara (Hippoboscidae s.l.), which I classify with the Glossinidae in the Hippoboscidae family-group. The other families of Calyptratae here recognized are the Scatophagidae, Anthomyiidae, Fanniidae, Muscidae and Tachinidae s.l. I do not include the Mormotomyiidae, which Hennig (1958) thought were aberrant Calyptratae.

Girschner (1893) was the first to conclude that the Scatophagidae should be included in the Calyptratae, basing his conclusion on characters of the chaetotaxy. But many taxonomists resisted this change and continued to classify the family among the "Acalyptratae". Girschner's views were vindicated by Frey (1921), who reached the same conclusion from analysis of an entirely different set of characters (the mouthparts). The structure of the male postabdomen and genitalia provides further strong evidence in support of the classification of the Scatophagidae in the Calyptratae, as indicated in my characterization above.

The name "Calyptratae" refers to the large squamae (= calyptrae) shown by many members of this group. However much variation is shown in the size of the squamae, and they are relatively small in the Scatophagidae and some members of other groups. Hennig (1965a) considers that the phylogenetic significance of size differences in the squamae is still obscure. Another character whose phylogenetic significance is in doubt is the presence or absence of sexual dimorphism in the size of the eyes and frons width. A greater or lesser degree of dimorphism in this respect is shown

by most species of all families except the Scatophagidae and the Hippoboscidae family-group. I think that such sexual dimorphism was present in the groundplan of the Schizophora (see above under Lonchaeoidea), but it is arguable that its presence in some families of Calyptratae is secondary (see Hennig, in press), since no dimorphism is apparent in the two groups just mentioned. I myself doubt the need to postulate secondary evolution of such sexual dimorphism in the Calyptratae, since such dimorphism is also well developed in a second group of Muscoidea, the Tanypezoinea. But I offer no firm opinion.

The question of how the Calyptratae should be subdivided has still not been settled. The primary subdivision should probably be either between the Scatophagidae and all other Calyptratae (as in the classification outlined by Hennig 1955: 2), or between the Hippoboscidae family-group and all other Calyptratae. The latter hypothesis was implied in the comments of Herting (1957) and is now favoured by Hennig (in press). These different interpretations of the relationships between the families of Calyptratae are implicated with possible alternative evaluations of certain character sequences. The following conditions shown by the Glossinidae can be interpreted as groundplan conditions of the Calyptratae, if the Hippoboscidae family-group is postulated to be the sister-group of all other Calyptratae: (1) 6th tergum (♂) unreduced, as long as 5th tergum (fig. 67); (2) 6th and 7th segments (♀) not retractile, with 7th pair of spiracles lying on 7th segment; (3) cerci (♂) not linked to telomeres; and (4) 7th right spiracle (♂) lying within 8th sternum (figs. 61 and 67). On the other hand there are grounds for suspecting that some of these conditions may be secondary, in particular because the development of secondary (pseudoplesiomorphous) conditions of the female postabdomen is well shown by certain larviparous

groups of Tachinidae s.l. Since all members of the Hippoboscidae family-group are macrolarviparous or pupiparous, the external structure of the female postabdomen in this group can be explained as the result of a similar series of modifications leading to a pseudoplesiomorphous condition; reduction of the male cerci may have been correlated with such changes in the structure of the female postabdomen. Only the unreduced male 6th tergum is difficult to explain as pseudoplesiomorphous; but the evidence of this condition seems inconclusive, since in some Scatophagidae the 6th tergum is not much shorter than in the Glossinidae.

The presence of the 7th right spiracle (♂) on the inverted 8th sternum is an undoubtedly apomorphous condition shown by members of all groups of Calyptratae except the Fanniidae (whose postabdominal morphology is evidently highly modified) and some Scatophaginae. In the latter group the position of the right postabdominal spiracles is variable. Both may be in the membrane of the genital pouch (*Cordilura latifrons* Loew); the 6th at the edge of the 6th tergum, the 7th in membrane (*Cordilura confusa* Loew); both within the 6th tergum (*Orthacheta* and *Spaziphora*); or the 6th within the 6th tergum, the 7th within the 8th sternum (*Pogonota* and *Scatophaga*). None of the species examined showed the arrangement characteristic of most other Calyptratae, in which the 6th right spiracle remains in membrane but the 7th right lies within the (inverted) 8th sternum. The question of whether the latter condition can be ascribed to the groundplan of the Calyptratae is thus implicated with whatever view is taken of the relationship between the Scatophaginae and other Calyptratae. Only if the former are postulated to be the sister-group of all other Calyptratae (including Delininae), is it reasonable to maintain that both the right postabdominal spiracles lay in membrane in the groundplan of the Calyptratae.

Movement of the 7th right spiracle onto the inverted 8th sternum can then be postulated as an autapomorphous groundplan condition of the second sister-group (other Calyptratae, including Delininae). Additional support for such an interpretation is provided by the relatively large size of the 6th tergum (♂) in Scatophaginae, to which Crampton (1944a) drew attention. As a further consequence of the interpretation that the Scatophaginae are the sister-group of all other Calyptratae, the following conditions may be attributed to the groundplan of the Calyptratae: (1) female postabdomen forming ovipositor which can be retracted within 5th segment (see Hennig 1965a: 6); (2) 7th abdominal spiracles (♀) displaced anteriorly, lying on or near posterior margin of 6th tergum (see the information presented by Herting 1957); and (3) cerci (♂) linked to telomeres (see Hennig, in press).

Salzer (1968) has described a link (articulation) between the telomeres and cerci in males of *Calliphora* (Tachinidae s.l.). I agree with Hennig's (in press) view that this condition can be ascribed to the groundplan of the Calyptratae as a whole, or possibly with the exclusion of the Hippoboscidae family-group (if the latter is the sister-group of all other Calyptratae). Such a link is absent in most other Schizophora, but I found a similar condition, probably through homoplasy, in the Diopsidae and a few genera of Heleomyzidae.

The classification of the Calyptratae proposed by Roback (1951) was incomplete, since he did not consider the Hippoboscidae s.l. Roback's paper provides much useful information, but I do not think that he gave sufficient justification for two of his main classificatory proposals, namely that the Scatophagidae ("Scopeumatinae") and Anthomyiidae be included in the "Anthomyiidae" in a widened sense, and that the "Anthomyiidae", Fanniidae

and Muscidae be included in a superfamily "Muscoidea". While the possibility that the "Muscoidea" and "Anthomyiidae" in Roback's sense are monophyletic groups cannot be excluded on present information, no positive evidence for this in terms of synapomorphous conditions has yet been offered. The characterization of these groups given by Roback refers to symplesiomorphous conditions or conditions whose phylogenetic significance has not been clarified. Therefore I accept Hennig's (1958) opinion that these proposals were not an improvement in the classification from the standpoint of phylogenetic systematics. The question of which of the groups here recognized as families are most closely related to one another is unlikely to be clarified until much more comprehensive information than hitherto is available on the Scatophagidae and Anthomyiidae.

The presence of the 7th right spiracle on the inverted 8th sternum in most male Calyptratae has caused some authors difficulty in interpreting the homologies of the sclerites. To clarify this question I therefore present this detailed note. At first sight my interpretation may seem self-contradictory, since although I claim to have shown that the 8th segment is inverted (see section 3.2), it is established that the 7th spiracles of Calyptratae are connected with the preceding spiracles on the same side in the normal manner (fig. 12). Crossing of the lateral tracheal trunks as a result of rotation within the puparium occurs only posterior to the last (7th) pair of spiracles. To understand this morphological paradox, it is necessary to consider the time sequence of the changes which occur within the puparium. Pihan (1969) has treated the development of the imaginal tracheal system of *Calliphora erythrocephala* Meigen within the puparium. He has unfortunately not stated the relationship of the sequence of tracheal development to the rotation of the terminal segments. But if

we assume that the speed of development was similar to that of Schröder's (1927) material of the same species, the synchronization appears to be roughly as follows. The terminal segments rotate on about the 5th day after pupation. At this time the larval tracheal epithelium has largely degenerated, but the imaginal tracheoblasts of the 4th to 7th abdominal segments are still small; the lateral commissures between them have not yet been regenerated, and (to judge from Pihan's figure) the adult spiracles have not yet been formed. The larval transverse spiracular commissures of the 8th abdominal segment have degenerated by this time and are not regenerated in the adult. The time of formation of the adult spiracles and their linking with the rest of the system was unfortunately not established precisely, but it seems unlikely that this occurred before the eighth day. At any rate, though the possibility of some degree of error in correlating two authors' experimental data must be admitted, it seems clear that the 7th abdominal spiracles are not formed until after the completion of rotation. Schröder (1927) makes no mention of spiracles, which presumably means that no trace of these was detected in his serial sections of specimens fixed during the course of rotation. Thus it appears that the completion of rotation before the formation of the terminal abdominal spiracles has allowed one of these (the 7th right) to develop on a rotated segment without any change in its relation to the preceding spiracles. The ends of the lateral trunks are rotated (after the 7th spiracles), because they develop from the epithelium of the larval tracheal trunks which are carried across one another by the rotation while in the process of regeneration.

Prefamily Micropezoinea

This group is equivalent to the Micropezoidea s.l. of Hennig (1958),

with the inclusion of the additional genera discussed by D. K. McAlpine (1966) and Hennig (1969a). I divide the group into three families: Cypselosomatidae, Neriidae and Micropezidae. I do not accept McAlpine's suggestion that the Megamerinidae may also belong to this prefamily. I refer that family to the Sciomyzoinea. The Micropezoina are well characterized as a monophyletic group by the following groundplan conditions which are apomorphous with respect to the groundplan of the Muscoidea:

- (1) Periandrium (♂) elongate (figs. 71 and 72); aedeagus borne on long basal cone ("Basalkegel des Aedeagus", Hennig 1958), which is strengthened by a pair of sclerites below ("x" on figs. 71-73) (the "st 2" of Hennig 1934 and 1936a) and an unpaired sclerite above ("y" on fig. 73) ("st 1" of Hennig 1936a).

The supporting sclerites in the basal cone of the aedeagus are usually absent in Taeniapterinae (Hennig 1934), but I think that they were secondarily lost here. They are usually present in all other families and subfamilies, and are particularly well developed in those genera in which the morphology of the postabdomen seems to be the most plesiomorphous in other respects (for instance *Micropeza* and *Heloclusia*). I therefore think it highly probable that these sclerites belong to the groundplan of the Micropezoina. The presence of these sclerites is probably an autapomorphous condition of the Micropezoina, since they have no demonstrated homologues in any other group.

- (2) Aedeagus (♂) elongate, largely supported by very long paraphalli (figs. 72 and 73).

This condition is correlated with the modifications of the genital segment stated above. In contrast with the Tephritoinea, with which the Micropezoina were classified by Hendel (1936), the aedeagus of Micropezoina is largely supported by long rigid paraphalli and cannot be coiled when at rest (except for the membranous terminal processes present in a few species). Protection of the aedeagus when at rest has been achieved by elongation of the genital segment. The sclerotization of the apical area of the aedeagus ("glans") is variable.

- (3) 6th sternum (♂) triangular, more or less symmetrical (fig. 71).

The condition of the 6th sternum shown by the Cypselosomatidae and Taeniapterinae (Micropezidae) is probably indicative of the groundplan condition for the Micropezoinea. In these groups the 6th sternum is triangular (with the apex of the triangle directed anteriorly) and more or less contiguous posteriorly with the 7th sternum. The latter is asymmetrically developed (extending dorsally on the left side, where it becomes fused with the inverted 8th sternum), as normally in Muscoidea. In Micropezinae and Calobatinae (Micropezidae) the 6th sternum is enlarged, but retains its triangular shape. This condition is probably a further modification of the postulated groundplan condition. Only in Neriidae does the derivation of condition of the 6th sternum seem problematical. In the single species studied by me the 6th sternum is rather small (like the preceding sterna) and widely separated from the 7th sternum by membrane. If the Neriidae and Micropezidae are monophyletic, I think that the reduced condition of the 6th sternum in Neriidae is probably apomorphous.

- (4) 7th tergum and sternum (♀) lengthened to form more or less closed ovipositor sheath (Hennig 1958).

This condition has been confirmed in the genera subsequently added to the Micropezoinea (under the family name Pseudopomyzidae) by D. K. McAlpine (1966) and Hennig (1969a).

The characteristic apomorphous conditions of the Micropezoinea are combined with certain noteworthy plesiomorphous conditions; in particular the retention of a large unmodified 6th tergum (♂) (all species) and the retention of the 7th and 8th tergum vestiges (♂) in at least some genera of each family. Hennig's and McAlpine's studies indicate that the recent members of the Micropezoinea are probably divisible into two sister-groups, the Cypselosomatidae (in which I include the Pseudopomyzidae) and the Micropezidae family-group (called "Micropezoidea s. str." by Hennig 1958).

Prefamily Australimyzoinea

The genus *Australimyza* is distributed in New Zealand (Harrison 1959), Australia (Colless and D.K. McAlpine 1970) and neighbouring subantarctic islands (Campbell Island, Antipodes Island and Macquarie Island) (Harrison

1959). Harrison classified the genus in the Milichiidae, but this is clearly untenable because the structure of the male postabdomen and genitalia of *Australimyza* is fundamentally different. The male postabdomen of *Australimyza* (figs. 74-76) retains a highly plesiomorphous structure, little removed from the postulated groundplan condition for the Muscoidea. The 6th tergum is unreduced, fully as long as the 5th tergum (as for instance in the Micropezoinea), and the asymmetrical 6th and 7th sterna are large and clearly defined. The aedeagal apodeme is free and rod-like. These plesiomorphous conditions are combined with some characteristic apomorphous conditions, as stated below. The combination of apomorphous and plesiomorphous conditions shown by *Australimyza* provides no basis for including the genus in any previously described family or in any of the other prefamilies of Muscoidea.

The Australimyzoinea (Australimyzidae) are characterized by the following apomorphous conditions with respect to the groundplan of the Muscoidea:

(1) Postverticals reduced.

According to Harrison (1959) the small postverticals may be parallel or slightly convergent or divergent.

(2) Vibrissae present.

(3) Costa broken twice, shortly beyond humeral crossvein and at end of subcosta.

(4) Subcosta contiguous or fused with vein r_1 apically.

(5) Spiracles 2-6 (σ) lying within margins of terga; 1st and 7th spiracles lost.

This characterization requires confirmation from study of additional species. In the species studied by me the spiracles are extremely small and difficult to locate. Only spiracles 2-6 could be traced.

- (6) 7th sternum (♂) and 7th tergum vestige fused both dorsally and ventrally, forming complete ring of sclerotization about 7th abdominal segment (figs. 74 and 75).

This condition is one of the most unusual modifications shown in the species studied by me. The sclerotization on the right side of the 7th segment consists of a narrow strip. In my opinion this represents the 7th tergum vestige, which is represented by a similar (but discrete) strip of sclerotization in certain other Muscoidea which retain highly plesiomorphous postabdominal structure (for instance some Micropezoinea and Coelopidae). I thus regard the condition of the sclerites of the 7th segment of *Australimyza* as a further modification of the groundplan condition of the Muscoidea. This modification consists of dorsal extension of the 7th sternum on the left side, so that this is fused with the 7th tergum vestige on the right side of the dorsum, as well as ventral fusion of the same two sclerites. A comparable dorsal fusion of the 7th sternum and 7th tergum vestige has evolved independently in *Helcomyza* (Dryomyzidae).

- (7) 8th tergum vestige lost (♂).
- (8) Periandrium (♂) divided into two halves (in other words, basimeres secondarily failing to meet across dorsum); telomeres more or less fused with periandrium, at most delimited by partial suture (fig. 76).
- (9) Aedeagus (♂) long and slender, supported by very long paraphalli (fig. 76).

In *Australimyza* the apex of the aedeagus is filamentous, without any indication of differentiated apical sclerites ("glans"). The base of the aedeagus can be swung against the aedeagal apodeme, as normally in Muscoidea.

Prefamily Diopsioinea

Hennig (1958) placed the two families which I include in this pre-family in his tentative group Nothyboidea. As previously discussed, I regard Hennig's Nothyboidea as heterogenous, and I present in this work a different classification of the included families. One clearly defined segregate of Hennig's "Nothyboidea" consists of the families Diopsidae and Syringogastridae. These are rather characteristically modified muscoid

flies occurring mainly in tropical regions. Their distribution is vicariant, for the Diopsidae have an Old World distribution centre (with a single species in North America), while the Syringogastridae are confined to the neotropical region.

The Diopsioinea are characterized as a monophyletic group by the following groundplan conditions which are apomorphous with respect to the groundplan of the Muscoidea:

- (1) Postvertical bristles absent.
- (2) Only one fronto-orbital (*ors*) and one vertical bristle (*vte*) present.

This groundplan condition is shown by the Diopsidae (see Shillito 1950 and Hennig 1958). In the Syringogastridae the remaining fronto-orbital has been lost.

- (3) Only one postalar bristle (*pa*) present (see Hennig 1965b and do Prado 1969).
- (4) 1st and 2nd abdominal terga fused, forming syntergum which is largest sclerite of abdomen; basal segments of abdomen (especially the 2nd segment) elongate, but distal segments short and wide, so that abdomen has petiolate appearance (fig. 77).

The characteristic petiolate appearance of the abdomen in Diopsioinea seems to be autapomorphous. The other groups included in Hennig's (1958) "Nothyboidea" all show a more uniform elongation of the abdominal segments, not a differential elongation of the basal segments.

- (5) 7th sternum (σ) forming complete ventral band of sclerotization, fused with inverted 8th sternum on right side (as well as on the left side as normally in Muscoidea) (fig. 77).

The structure of the male postabdomen of *Centrioncus* (the sister-group of all other recent Diopsidae) is readily explicable as a modification of the arrangement of postabdominal sclerites in the groundplan of the Muscoidea. In *Centrioncus* the expanded area of the 7th sternum on the left side is clearly delimited (fig. 78), as in most Muscoidea. But the condition shown by *Centrioncus* is apomorphous in respect of extension of the 7th sternum towards the right side, so that it forms a complete ventral band of sclerotization (fig. 77). In the other Diopsidae studied by me the sclerotization of the 7th and 8th segments is much reduced, and the ventral band is incomplete. However, the condition shown

by *Centrioncus* accords well with that described for the Syringogastridae (do Prado 1969), in which a complete ventral band is also present. Therefore I think it probable that the presence of the ventral band can be ascribed to the groundplan of the Diopsioinea. Do Prado does not refer in his text to an expanded area of the 7th sternum on the left side in Syringogastridae, but his figure of *Syringogaster lanei* do Prado (fig. 12), if I interpret it correctly, indicates that such an area is delimited (as in *Centrioncus*). In most other Muscoidea in which a complete ventral band of postabdominal sclerotization is formed, this condition has been achieved through expansion and fusion of the 6th sternum with the 7th and 8th sterna, although a similar ventral band formed by sclerites of the 7th segment is shown by some Cypselosomatidae. It is noteworthy that in the Diopsioinea the 6th sternum is not involved in the formation of the ventral band. In *Centrioncus* it remains large and is slightly more expanded on the left side (as normally in Muscoidea). Do Prado (1969) indicates that in Syringogastridae the 6th sternum is represented by a pair of small sclerites which are discrete from the ventral band.

(6) 7th and 8th tergum vestiges (♂) lost.

(7) 7th left spiracle (♂) within 7th sternum.

This condition is shown by the Syringogastridae and by *Centrioncus* (Diopsidae). In *Diopsis* and *Sphyracephala* the 7th left spiracle lies in membrane, but this condition may be secondary, consequent upon reduction of the sclerotization of the 7th and 8th segments.

(8) Aedeagus (♂) rather short, with complex distal section bearing lobes or processes (figs. 79 and 80).

I am not sure what other group of Muscoidea is most closely related to the Diopsioinea. Hennig (1958) suggested possible synapomorphies with the Megamerinidae (in which *Syringogaster* was formerly included) in respect of the loss of certain frontal bristles. However I doubt whether this interpretation is correct, as it is difficult to reconcile with the evidence of other characters. The structure of the male postabdomen in the Megamerinidae (fig. 97) is very different, and I provisionally classify that family in the Sciomyzoinea in this work. In the Diopsioinea the 6th abdominal segment in the male is scarcely reduced in comparison with the preceding segments, a plesiomorphous condition comparable with that shown, for instance, by the Micropezoina and Tanypezoinea. But in Megamerinidae the sclerites of the 6th segment (♂) are much reduced. The female postabdomen

of Diopsioinea does not show the elongation of the terminal segments characteristic of the Megamerinidae (see the figures given by Hennig 1958).

Prefamily Sciomyzoinea

I include in this group all the families referred to it by Hennig (1958) (as Sciomyzoidea), and tentatively add two small families, the Cremifaniidae and Megamerinidae. The Cremifaniidae were not considered in Hennig's (1958) analysis; the Megamerinidae were included in his group "Nothyboidea", which was heterogenous in my opinion. The complete list of families now referred to the Sciomyzoinea is as follows: Coelopidae, Phaeomyiidae, Dryomyzidae, Sciomyzidae, Helosciomyzidae, Ropalomeridae, Sepsidae, Megamerinidae and Cremifaniidae.

The reservations expressed by Hennig (1958, 1965b) on the validity of this group still remain. The families included here show many plesiomorphous conditions for the Muscoidea, and I am not able to give any convincing characterization in terms of autapomorphous conditions. The included families show, at least in their groundplan, the following conditions which according to Hennig's (1958) analysis are probably plesiomorphous (groundplan conditions of the Muscoidea): (1) the costa is unbroken, (2) the subcosta is complete, (3) the anal vein reaches the wing margin (except Sepsidae and Cremifaniidae), (4) vibrissae are absent or only weakly differentiated (in Sepsidae and Ropalomeridae), and (5) divergent postverticals are present (except Helosciomyzidae and Megamerinidae). The only possibly synapomorphous condition which I can put forward is:

- (1) 6th tergum (♂) somewhat shortened, not more than half length of 5th tergum.

The best developed 6th tergum among the species studied by me is that of *Heterocheila* (here provisionally referred to the Coelopidae), in which the 6th tergum is about half as long as the 5th tergum (fig. 82).

However, reduction of the 6th tergum is so widespread among the Muscoidea that little reliance can be placed upon this condition in isolation. In view of this lack of satisfactory characterization, the Sciomyzoinea as presently understood must be considered a group whose limits require further investigation. Pending clarification, it is convenient to maintain this group in the classification, since there is no evidence that the included families are more closely related to groups outside the Sciomyzoinea than to each other.

J. F. McAlpine (1963) treated the Sciomyzoinea and Lauxanioidea as monophyletic, and this is also implied in the classification of Colless and D. K. McAlpine (1970). However, J.F. McAlpine did not demonstrate synapomorphous conditions in support of this view. The classification of these two groups together is difficult to reconcile with the presence of the typical muscoid morphology of the male postabdomen in Sciomyzoinea. In Lauxanioidea the structure of the male postabdomen is different (see above), and the mechanism for swinging the aedeagus against its apodeme is not developed.

Prefamily Anthomyzoinea

The families included in this group were mostly treated as families of uncertain relationship by Hennig (1958), except for the Sphaeroceridae, which he classified in the "Milichioidea". In subsequent works Hennig has tentatively proposed a superfamily Anthomyzoidea, for reception of (according to his latest treatment in the paper now in press) the Clusiidae, Acartophthalmidae, Anthomyzidae, Opomyzidae, Chyromyidae, Aulacigastridae, Asteiidae, Teratomyzidae and Periscelididae. On the basis of my studies of the male postabdomen and genitalia I conclude that the Teratomyzidae and Periscelididae

should be excluded from this consideration, as they belong to the Nothyboidea. The remaining families belong to the Muscoidea in the sense of this work, and they show many conditions in common. Probably most of these families are rather closely related and can be validly grouped in a prefamily Anthomyzoinea. But the limits of this prefamily are still very much in doubt. I propose to exclude the Clusiidae and Acartophthalmidae, since they are probably more closely related to families outside the Anthomyzoinea (see below under Agromyzoinea and Tephritoinea). On the other hand, I propose to add to the Anthomyzoinea the Heleomyzidae, Rhinotoridae, Borboropsidae and Trixoscelididae (grouped together by some authors as "Heleomyzidae" in the widest sense), all still treated by Hennig (in press) as groups of uncertain relationship. These families show all the conditions which can be suggested as groundplan conditions of the Anthomyzoinea if they are excluded, with the exception of shortening of the anal vein; and, in particular, their possession of setose postgonites seems to me to provide evidence that they should be included in the Anthomyzoinea, since I have not found this condition in any other group of Muscoidea. The Sphaeroceridae should also be referred to the Anthomyzoinea, since the structure of their male genitalia indicates that they are closely related to the Chyromyidae and Aulacigastridae and were misplaced in Hennig's "Milichioidea" (included in Tephritoinea in this work). The complete list of families here referred to the Anthomyzoinea is as follows: Heleomyzidae, Rhinotoridae, Anthomyzidae, Borboropsidae, Trixoscelididae, Asteiidae, Opomyzidae, Sphaeroceridae, Chyromyidae and Aulacigastridae.

The Asteiidae are possibly misplaced in the Anthomyzoinea, since they show the following conditions differing from the postulated groundplan conditions of this prefamily: (1) postverticals parallel or divergent, (2) costa unbroken, and (3) postgonites not setose. On the

other hand, these conditions are possibly secondary. Pending clarification I follow Hennig's classification of this family in the Anthomyzoinea.

If the Anthomyzoinea in my present sense are monophyletic, they may be characterized by the following conditions in their groundplan which are apomorphous with respect to the groundplan of the Muscoidea:

(1) Postverticals convergent.

The postverticals are convergent in the groundplan of most of the families here included in the Anthomyzoinea, and I therefore ascribe this condition to the groundplan of the Anthomyzoinea. But the postverticals are reduced or absent in the groundplans of the Opomyzidae, Asteiidae and Aulacigastridae. Long divergent postverticals are shown only by the problematical genus *Stenomiera* (? Anthomyzidae).

(2) Vibrissae present.

Vibrissae are absent only in the Opomyzidae.

(3) Costa broken at end of subcosta.

Among recent Anthomyzoinea the costal break is absent only in the Asteiidae. Hennig (1965b, 1967) referred to the Anthomyzidae two species from Baltic amber in which the costa appears to be unbroken (*Protanthomyza* and *Xenanthomyza*), but it is evident from his remarks that the classification of these insects is problematical.

(4) 6th tergum (♂) somewhat shortened, at most two-thirds length of 5th tergum.

(5) Postgonites (♂) setose.

This character has not previously been considered. I find that the postgonites bear several setulae in some or all the species studied of most of the families here included in the Anthomyzoinea, with the exception of the Asteiidae and Opomyzidae. In the latter the postgonites are absent. I did not find such setose postgonites in any other group of Muscoidea. I am satisfied that these structures are postgonites, since at least in some species they are turned outwards when the aedeagus is swung into the copulatory position, an action which can be observed, for instance, in the postgonites of Agromyzidae.

Hennig (in press) discusses the widespread occurrence of hook-shaped antennae ("Hakenfühlern") among the Anthomyzoinea. Clearly such conditions should be considered in future studies of the Anthomyzoinea, and they may

assist in defining some of the included groups. But there are still doubts about whether hook-shaped antennae should be ascribed to the groundplan of some of the families.

Members of the Anthomyzoinea exhibit a variety of conditions of the aedeagus, and it is not now possible to define the groundplan condition. In the Anthomyzidae and most genera of Heleomyzidae the aedeagus is elongate. However, in the Suillinae (Heleomyzidae) the distal part of the aedeagus is broad and flattened. An undoubtedly apomorphic condition is shown by the Rhinotoridae, in which the aedeagus is posteriorly directed, with the swinging mechanism lost. The Borboropsidae, Chyromyidae, Sphaeroceridae and Aulacigastridae are all characterized by a short aedeagus with very complex sclerotization. It is not clear whether the various types of broad aedeagus should be considered apomorphic or plesiomorphic in relation to the more elongate conditions shown by the Anthomyzidae and most Heleomyzidae.

In addition to the groups here recognized as families, Hennig (in press) also refers to the Anthomyzoinea the South American genera *Schizostomyia*, *Gayomyia* and *Paraleucopis*. None of these is known to me. Steyskal kindly sent me a sketch of the male postabdomen of *Schizostomyia*, which indicates that this genus shows the asymmetrical arrangement of the postabdominal sterna characteristic of the Muscoidea and a reduced 6th tergum (represented only by a narrow band). The validity of Hennig's exclusion of *Schizostomyia* from the Psilidae (Nothyboidea) is thus confirmed. The genus clearly belongs to the Muscoidea, but I am unable to give an independent opinion on whether it belongs to any family of Anthomyzoinea without further information.

Prefamily Agromyzoinea

In this group I include the Agromyzidae and the Clusiidae. The relationships of the Agromyzidae have been variously interpreted. Most authors have suggested that they are closely related to one or other family of Tephritoinea, in particular to the Tephritidae, Odiniidae or Milichiidae. Hennig (1965b) accepted the view that the Odiniidae and Agromyzidae are sister-groups, although admitting that there are no decisive grounds for this interpretation. In my opinion these families are unlikely to be sister-groups, because the aedeagus of Odiniidae shows a condition which seems derived from that which I ascribe to the groundplan of the Tephritoinea. The only apomorphous conditions which support the hypothesis of a sister-group relationship between the Odiniidae and Agromyzidae are either widespread (such as inwardly directed *ori*, costal break present, anal vein shortened, two spermathecae) or proportional changes (namely the presence of a long aedeagal apodeme and hypandrium in both families, to which Spencer 1969 refers). I suggest that the sister-group of the Agromyzidae is more probably the Clusiidae. The agreement in frontal chaetotaxy and wing venation between the Agromyzidae and Clusiidae is no less than that between the Agromyzidae and Odiniidae; and the Clusiidae show a type of aedeagus which is similar to that of the Agromyzidae in respect of length and complexity of sclerotization. In respect of most character sequences analysed the Clusiidae are more plesiomorphous than the Agromyzidae. The latter family is highly divergent in some respects from all other Muscoidea, which is the reason why judgement of its relationship is difficult.

If the Clusiidae and Agromyzidae are correctly grouped in the Agromyzoinea, then this prefamily seems characterized in its groundplan by the

following conditions which are apomorphous with respect to the groundplan of the Muscoidea:

- (1) Aedeagus (♂) extremely elongate, with complex sclerotization including phallopore, paired paraphalli and distal sclerites of varying form; epiphallus well developed (figs. 118 and 121).

The term paraphalli in the above characterization refers to the sclerites which have been called the "arms of the basiphallus" by workers on Agromyzidae. In the Agromyzidae and most Clusiidae the mechanism for swinging the aedeagus against its apodeme is well developed, as in the groundplan of the Muscoidea, so that the aedeagus is anteriorly directed when at rest. But in *Clusiodes* (Clusiidae) this mechanism has been lost, and the aedeagus remains more or less posteriorly directed when at rest. The latter condition is clearly apomorphous, not belonging to the groundplan of the Clusiidae. Members of the Agromyzoinea display some of the largest and most complexly sclerotized aedeagi among the whole of the Diptera. In some Clusiidae the basal area of the aedeagus is somewhat flexible and coiled when at rest, a condition approaching that shown by Tephritoinea. However, this condition is not shown by the Agromyzidae, in which the basal section is always supported by rigid paraphalli; it seems unlikely that such coiling can be ascribed to the groundplan of the Agromyzoinea.

An epiphallus was clearly present in the groundplan of the Agromyzoinea. According to D. K. McAlpine (1960) such a structure is absent among the Clusiidae only in *Clusiodes*, which has highly modified genitalia due to loss of the swinging mechanism. In *Clusia* (fig. 118) the epiphallus is a large upcurved posterior process of the phallopore, which is open below (not fully cylindrical as in Agromyzidae). In Agromyzidae the epiphallus is discrete from the phallopore and has a complex structure.

- (2) 8th tergum vestige lost (♂).

The male postabdomen of Clusiidae shows the asymmetrical pattern of sclerites typical of the Muscoidea. Of the sclerites present in the groundplan of the Muscoidea, only the 8th tergum vestige has been lost.

- (3) 8th abdominal segment (♀) elongate and largely membranous, forming a retractile ovipositor which is retraced within subconical 7th segment when at rest.

The condition of the female postabdomen shown by the Clusiidae is clearly more plesiomorphous than the characteristic boring ovipositor of the Agromyzidae. A retractile ovipositor occurs in other groups of Muscoidea (such as the Calyptratae, Tanypezoinea and Tephritoinea), and it is possible that some of these resemblances may be due to synapomorphy. But no firm

judgement can be made until more extensive comparative studies on the female postabdomen of Muscoidea are available. I have noted that in a preparation of *Clusiodes melanostoma* (Loew) the small 8th sternum is entire, not divided as in the Tephritoinea and Calyptratae.

- (4) Two spermathecae (♀) (Sturtevant 1926, Hennig 1958, Saskawa 1958).
- (5) Vibrissae present (Hennig 1958).
- (6) Inwardly directed lower fronto-orbital bristle (*ori*) present.

The number of fronto-orbital bristles is variable in the Clusiidae, and I find no clear statement of the groundplan condition in the literature. However, the presence of a pair of inwardly directed *ori*, in addition to two or more upwardly directed orbitals, is common to the majority of species (see Hennig 1958, figs. 190-194). The groundplan condition for the Agromyzidae is clearly one in which two pairs of upwardly directed *ors* are present, and one or two pairs of inwardly directed *ori*. Deviations from this pattern occur only in a small minority of species.

- (7) Costa broken at end of subcosta.

Hennig (1958) postulated that the costa was unbroken in the groundplan of the Clusiidae, as in *Heteromeriingia*. However, D. K. McAlpine (1960) states that the costa was incised in the material of *Heteromeriingia* seen by him, as in all other Clusiidae known to him.

Prefamily Tephritoinea

I include in this prefamily the Otitoidea, Pallopteroidea (except Lonchaeidae) and part of the Milichioidea of Hennig's (1958) classification, as well as the families Chloropidae, Chiropteromyzidae, Mormotomyiidae, Cnemospathidae, Acartophthalmidae and Odiniidae, which were unplaced in Hennig's classification. I do not include in this prefamily the Braulidae, Canacidae and Sphaeroceridae, which Hennig tentatively placed in the "Milichioidea". In this work I refer the Sphaeroceridae to the Anthomyzoina, and treat the Braulidae and Canacidae as families of uncertain relationship. The complete list of families here referred to the Tephritoinea is as follows: Chiropteromyzidae, Mormotomyiidae, Cnemospathidae,

Odiniidae, Tethinidae, Acartophthalmidae, Carnidae, Milichiidae, Chloropidae, Conopidae, Eurygnathomyiidae, Richardiidae, Piophilidae s.l. and Tephritidae s.l.

Speight (1969) and Colless and D.K. McAlpine (1970) have proposed to classify the Tethinidae, Milichiidae and Chloropidae in the Drosophiloidea, but I am convinced that this is incorrect. The Chloropidae include some genera, such as *Lasiopleura*, in which the asymmetrical structure of the male postabdomen characteristic of Muscoidea is retained. The simpler symmetrical structure shown by the closely related Milichiidae thus cannot be derived from the groundplan condition of the Drosophiloidea. The structure of the male postabdomen and genitalia in the Carnidae, which probably belong to a monophyletic group containing also the Milichiidae, Chloropidae and Acartophthalmidae, is hardly separable from that of some of the groups included by Hennig in the Otitoidea and Pallopteroidea. I think it most improbable that the complex and highly modified type of aedeagus concerned was evolved independently in different lineages, and no incompatibility with the evidence of other characters arises from postulating that this type of aedeagus indicates common ancestry in every case. The impossibility of drawing any clear distinction in respect of the structure of the male postabdomen and genitalia between the Chloropidae family-group and the families included in Hennig's Pallopteroidea and Otitoidea is further emphasized by the structure of the Chiropteromyzidae and Cnemospathidae. These show the same characteristic type of aedeagus, but would be excluded from Hennig's Pallopteroidea and Otitoidea, as well as from the Chloropidae family-group, on account of the less apomorphous condition of the female postabdomen. In my opinion a wider group is needed to embrace these families, as well as the Chloropidae family-group and

Hennig's Pallopteroidea (except Lonchaeidae) and Otitoidea. The name Tephritoinea is here proposed in a wide sense for a group of this kind.

The Tephritoinea are characterized as a monophyletic group by the following groundplan conditions which are apomorphous with respect to the groundplan of the Muscoidea:

- (1) Aedeagus (♂) extremely elongate, flexible, coiled at rest, extended by pressure of body fluid, with numerous fine cuticular processes ("pubescence") (figs. 123, 130, 131, 134, 138 and 145).

In other Muscoidea the aedeagus is usually relatively rigid, and is extruded primarily by contraction of muscles originating on the aedeagal apodeme, which causes the aedeagus to swing about its attachment to the apodeme. This swinging mechanism is clearly retained in most Tephritoinea (except Odiniidae and Conopidae), since the base of the aedeagus articulates with the aedeagal apodeme in the normal manner and a distinct phallosome is usually present. But some form of pumping action is clearly also required to produce stiffening and straightening of the extremely long aedeagus, which is flexible and coiled when at rest. Hanna (1938) suggested that erection of the aedeagus in *Ceratitis* (Tephritidae) is achieved by pressure of the seminal fluid in the ejaculatory duct produced by contraction of the muscles of the ejaculatory bulb. But it is unclear whether his conclusion was based on observation, and Munro (1947: 73) has questioned the accuracy of Hanna's work. I doubt whether the volume of seminal fluid would be sufficient to stiffen and straighten the aedeagus; more probably this result is achieved by pumping of body fluid. In many Tephritoinea a pair of sclerotized rods is present in the wall of the aedeagus. I suggest that these represent the paraphalli of other Muscoidea, and that the coiled aedeagus of Tephritoinea has been derived from a less modified muscoid type of aedeagus by progressive increase in the length and elasticity of this organ. When at rest the aedeagus is either coiled within a genital pouch on the right side of the postabdomen, or is looped around the dorsum of the postabdomen from the right side. The latter condition is shown by the Chiropteromyzidae, Cnemospathidae, and some of the groups included in Hennig's Otitoidea and Pallopteroidea. The aedeagus is usually clothed with fine "pubescence", a characteristic condition which should probably be ascribed to the groundplan of the Tephritoinea on account of its wide distribution. In a few groups the cuticular processes are strongly sclerotized, and are more appropriately called "spinules" rather than "pubescence".

- (2) 7th and 8th abdominal segments (♀) elongate, forming slender retractile ovipositor; 8th sternum divided into paired longitudinal sclerites.

It has been the frequent practice in classifications of the Schizophora to define a group partly coinciding with the Tephritoinea in my present sense on the basis of the structure of the ovipositor. For instance, Hendel (1936) characterizes his "Trypetides" with the words "Basalstück des Ovipositors zu einem chitinierten Tubus verwachsen". Hennig's Otitoidea were similarly characterized ("Beim Weibchen 7. Abdominalsegment zu einer Legrohrscheide umgebildet"). However such characterization applies to only part of the Tephritoinea in the present sense. The condition which I ascribe to the groundplan of the Tephritoinea is in my opinion an earlier stage in the character sequence leading to the type of ovipositor described in the above quotations.

Some degree of retractility of each segment into the preceding segment is a general feature of the abdomen in Diptera. The formation of a "retractile ovipositor" involves lengthening of the genital segment (segment 8) and strengthening of the retraction mechanism, so that the genital segment can be fully retracted despite its increased length. The groundplan condition for the Tephritoinea appears to be one in which both the 7th and 8th segments are elongate, with the distal part of the 7th segment being largely membranous and becoming infolded as the 8th segment is retracted; the sclerites of the 7th segment remain more or less unmodified as dorsal and ventral plates on the anterior part of the segment. Such a condition occurs, for instance, in the Chiropteromyzidae and Cnemospathidae. Two different trends of further modification from the groundplan can be seen. In some groups (notably the Odiniidae, Carnidae and Chloropidae) the 7th sternum or both the sclerites of the 7th segment are somewhat reduced, so that the preceding segments become the effective sheath for the ovipositor. In other groups the sclerites of the 7th segment are enlarged and sometimes fuse to form a conspicuous ovipositor sheath (or "basal cone" of the ovipositor), which is the condition used by Hennig (1958) to characterize his group Otitoidea.

Secondary shortening of the ovipositor occurs at least in *Meromyza* (Chloropidae) and in *Pelomyia* (Tethinidae). I did not undertake an extensive survey of the structure of the ovipositor, and undoubtedly much useful information for purposes of classification could be obtained from further studies.

(3) "*Musculus hypandriotergalis*" lost (?).

In my discussion above of the characterization of the Muscoidea I have put forward the hypothesis that this unpaired muscle (linking the hypandrium with the inverted 8th sternum on the left side) was present in the groundplan of the Muscoidea. This muscle has not been reported for any Tephritoinea. It may be definitely recorded as absent from the tephritid *Urophora* (= *Euribia*) (Hennig 1936a), from *Thecophora* (Conopidae) and from *Chlorops* (Chloropidae); the latter two records are based on serial sections in my possession. Of course my ascription of loss of this muscle to the groundplan of the Tephritoinea is only tentative in view of the limited information.

(4) Costa broken at end of subcosta (or near end of r_1 if subcosta reduced).

Different conditions of the costa occur only among the Acartophthalmidae, Conopidae and Tephritidae s.l. The almost universal presence of a single costal break at the end of the subcosta in all other families suggests that this is the groundplan condition for the Tephritoinea.

I agree with Hennig (1958) that the presence of a spur ("Zipfel") on the anal cell in some groups of Tephritidae s.l. is apomorphous. A recurved cross-vein is shown by most other Tephritoinea which retain a long anal vein, including Chiropteromyzidae, Cnemospathidae, *Hemeromyia* (Carnidae), Acartophthalmidae and Eurygnathomyiidae.

The conditions of the male postabdominal sclerites in Tephritoinea can be arranged in a sequence leading from the groundplan condition of the Muscoidea (with the 6th tergum and vestiges of the 7th and 8th terga retained) to the much simpler types of structure shown, for instance, by the Tethinidae, Milichiidae, Conopidae and Acartophthalmidae.

The Tephritoinea contain two subordinate groups which are dominant in the recent fauna, each containing thousands of species. These are the Tephritidae family-group (equivalent to the Pallopteroidea and Otitoidea of Hennig 1958) and the Chloropidae family-group. But there are also several smaller families of Tephritoinea not referable to these groups, and it does not seem possible to make a dichotomy of the Tephritoinea on present information.

My reference of the Conopidae to the Tephritoinea was foreshadowed by the comments of Hennig (1952a), although he did not follow up this question in later works. Formerly the family was sometimes thought closely related to the Syrphidae, and was still classified in the Syrphoidea in Stone *et al.* (1965). However, such a classification is untenable, since it has been known at least since the 1880's that the Conopidae possess a ptilinum. Recently the most widely held opinion has been that the Conopidae

are the sister-group ("Archischiza") of other Schizophora ("Muscaria"). This classification has generally been credited to Enderlein (1936), although in fact Brauer (1890) proposed the same group concepts under different names. Enderlein's names have been tentatively accepted in recent works of Hennig (1958, 1966b). The grounds for Enderlein's view were not clearly stated. He merely remarked that the Conopidae "Besitz der Stirnspalte mit Charakteren der Aschiza verbinden", without specifying which characters of the "Aschiza" he meant. The resemblances in wing venation between the Syrphidae and some Conopidae (notably the elongate anal cell) are not shown by all members of the Conopidae and are probably secondary. The reduction or absence of frontal bristles in most recent Conopidae is also clearly secondary, since both *Myopa* and the Baltic amber fossil *Palaeomyopa* retain an arrangement of frontal bristles typical of the Schizophora. Hennig (1958) suggested that the short length of the ptilinal suture might be a plesiomorphous condition of the Conopidae, an interpretation originally suggested by Brauer (1890). But this interpretation is also doubtful, since Hennig has subsequently reported (Hennig 1966b) that some Conopidae, such as *Dalmannia*, have a suture no shorter than in most other Schizophora. As for the structure of the ptilinum itself, Strickland (1953) reported that the ptilina of Conopidae "are voluminous and represent the most rugged type of ptilinum which we have encountered". Thus no relatively plesiomorphous conditions have been found in the Conopidae to support the classification of this family as the sister-group of all other Schizophora.

In my opinion the Conopidae are probably referable to the Tephritoinea, since some genera show the type of aedeagus which I ascribe to the ground-plan of this prefamily. Hennig (1966b) was led by his acceptance of

Enderlein's classification to postulate that the long pubescent aedeagus of the conopid genera *Dalmannia*, *Parazodion* and *Paramyopa* was the result of convergence with the condition in Tephritoinea. The need to postulate convergence is removed, if it is accepted that Enderlein's division of the Schizophora into "Archischiza" and "Muscaria" was unwarranted. The aedeagus of *Dalmannia* (fig. 138) is long and flexible, with conspicuous pubescence, coiled when at rest; the paraphalli are retained as a pair of lateral strips, and apically the aedeagus is somewhat expanded to form a weak "glans". This structure is typical of the Tephritoinea, and I doubt that such a complex condition was evolved independently in the Conopidae. The short, largely membranous aedeagus of the Conopinae may be due to secondary reduction. Similar considerations apply to the structure of the female ovipositor. In *Dalmannia* the 7th and 8th abdominal segments form an elongate ovipositor (Streiff 1906: 199), as also in *Stylogaster*. But in Conopinae the 8th segment is short. I suggest that a secondary shortening of the ovipositor has occurred in Conopinae, correlated with shortening of the aedeagus.

6.3. Key to the families of Schizophora

The key below is not intended for quick sorting of material, since some of the characters used can only be seen in preparations. It is intended primarily to provide systematists with a first approximation of where doubtful species should be classified. The key can be used for males alone, or for males and females in association; but not for females alone.

The keys hitherto available include early divisions on the basis of such characters as the presence or absence of the costal break and vibrissae, and the direction of the postvertical bristles. Since these

characters are subject to variation within some groups, such divisions in the key do not reflect the relationships between the families; and radical misclassification can occur because the distinctions drawn are equivocal in some cases. In the past many genera and species, particularly from the tropics, have been described in the wrong families due to the inadequacies of the available keys and an absence of comprehensive structural information of the kind which I have tried to present in this work. For these reasons I think there may be some value in my presenting an alternative key which makes extensive use of characters of the male postabdomen.

The best previous key to the families of Schizophora with worldwide coverage is that given by Hendel (1936).

KEY

- 1. Adults parasitic or phoresic, with enlarged or pectinate claws. Often wingless or brachypterous; if with functional wings (some Hippoboscidae), three radial branches crowded on fore-margin of wing and costa not extending beyond r_{4+5} 2
- Adults not parasitic or phoresic, except for a few Milichiidae and Carnidae (in which wing venation not of above type); if blood-sucking, not remaining on host. Usually with functional wings; if brachypterous (e.g. *Mormotomyia*, some Sphaeroceridae), claws not modified for clinging 3
- 2. Small (1 - 1.5 mm.) phoresic commensals of honeybee (*Apis*). Mouthparts not piercing. Wings, halteres and scutellum lost. Claws pectinate. Male abdomen with series of six pleural sclerites between terga and sterna (fig. 31) Braulidae

- Larger, blood-sucking parasites of birds and mammals, with piercing mouthparts. Scutellum present. Claws enlarged, hook-shaped. Male abdomen without pleural sclerites, often with much reduced sclerotization. Apterous, brachypterous or fully winged
- Hippoboscidae (*sensu lato*)
(compare the closely related Glossinidae, couplet 26)

Note. Individuals of *Carnus* (Carnidae) which have shed their wings may also be taken to this couplet. The mouthparts of *Carnus* are short, not adapted for piercing.

- 3. Uniformly dark flies with dark halteres. Frons densely clothed with setulae, at most with single *ors*. Female abdomen with normal terga and sterna only as far as 6th segment. Male aedeagus posteroventrally directed at rest, rigid and uniformly sclerotized, often upcurved (figs. 21 and 23)
. (Lonchaeoidea) 4
- Halteres usually pale; if dark (some Milichiidae and Agromyzidae), more than one *ors* present 5
- 4. Arista present; 2nd antennal article with suture; *ors* present; 7th abdominal segment (♀) extensively sclerotized, forming oviscape Lonchaeidae
- Arista lost; 2nd antennal article without suture; *ors* scarcely differentiated; female postabdomen membranous after 6th segment Cryptochetidae
- 5. Frons usually with one or two reclinate *ors* and single proclinate *ors* (except in some Ephydriidae); postverticals convergent (except in some Ephydriidae); 2nd antennal article with suture. Male postabdomen fully symmetrical, with 8th sternum

reduced to pair of dorsolateral vestiges or completely lost;
aedeagus not swung through wide arc against aedeagal apodeme.

(Groups of Ephydriidae in which the chaetotaxy of the head is
not as stated above may be recognized *inter alia* by loss of
the anal cell and lower cross-vein, and by the sclerotized
ventral receptacle (♀); see couplet 6)

. (Drosophiloidea) . . . 6

- Frontal chaetotaxy not as stated above, except in some
Milichiidae. Other conditions not shown in combination . . .

. 10

6. Spermathecae (♀) rudimentary; ventral receptacle heavily
sclerotized. 6th and 7th terga (♂) very narrow (*Diastata*,
fig. 41) or lost (other genera). 7th abdominal spiracles lost
in both sexes. Anal vein and anal cross-vein usually absent
(except in *Diastata*) Ephydriidae

- Two spermathecae (♀) present; ventral receptacle not sclero-
tized. Anal cell closed except in Camillidae 7

7. 5th and 6th terga (♂) reduced (fig. 35); 4th segment largest
abdominal segment. Female postabdomen largely membranous.
Anal vein and anal cross-vein lost. 7th abdominal spiracles
absent from both sexes Camillidae

- 5th tergum (♂) large. 6th and 7th segments (♀) with well
developed terga and sterna 8

8. Aedeagus (♂) grossly enlarged (fig. 40). Subcosta distinct
to wing margin Curtonotidae

- Aedeagus (♂) not as above. Subcosta faded or fused with r_1
distally 9

9. 6th and 7th terga (♂) discrete (fig. 37). Proclinate *ors* lying between reclinate *ors* and eye margin Campichoetidae
- 6th and 7th terga (♂) fused, forming large syntergum (fig. 33). Proclinate *ors* lying before or to inner side of reclinate *ors* Drosophilidae
10. Aedeagus (♂) sheathed dorsally by elongate aedeagal mantle, near apex of which lies pair of small postgonites; protandrial segments much reduced, at most with single dorsal sclerite between 5th segment and hypopygium (figs. 149-151). Female postabdomen modified for boring, with 6th tergum and sternum fused as sclerotized ring and 7th segment fusiform (with large tergum and sternum only narrowly separated by membrane) Fergusoninidae
- Aedeagus (♂) not as stated above. If female with boring ovipositor, 6th tergum and sternum discrete or reduced (some Tephritidae) 11
11. Aedeagus (♂) short; postgonites joined above aedeagus by pubescent fold (aedeagal mantle); postabdomen symmetrical, with only single dorsal sclerite between 5th segment and hypopygium (figs. 147-148). Female with hook-shaped cerci. *Ors* all inclined outwards over eye margin Canacidae
- Male genitalia not as above. Female cerci not hook-shaped 12

Note. Certain South American genera with hook-shaped female cerci (e.g. *Dihoplomyza*) cannot be taken beyond this couplet. Their family position is unclarified.

12. Hypandrium (♂) with pair of slender ventral processes; cerci

- fused below anus; aedeagus posteroventrally directed at rest (not swung through wide arc against aedeagal apodeme); post-abdomen symmetrical, with all sclerites of 7th and 8th segments lost (6th tergum last dorsal sclerite before hypopygium) (figs. 152-154) Notomyzidae
- Hypandrium (♂) without such ventral processes; other conditions stated above not shown in combination 13
13. Aedeagus (♂), when well developed, of simple tubular structure, posteroventrally directed at rest (not swung through wide arc against aedeagal apodeme); 7th tergum usually developed as dorsal sclerite (lost only in some Chamaemyiidae); sclerites of 8th segment lost (figs. 24-30). Costa unbroken; anal vein not extending to wing margin. Postverticals, when well developed, convergent (Lauxanioidea) . . . 14
- Aedeagus (♂) in most groups swung through wide arc against aedeagal apodeme to anteriorly directed rest position (see figs. 52-53). If not, other conditions stated above not shown in combination 16
14. 6th tergum (♂) much shorter than preceding terga; periandrium without discrete telomeres (fig. 30). 4 spermathecae (♀). Subcosta contiguous with r_1 before its apex Chamaemyiidae
- 6th tergum (♂) about as long as preceding terga; periandrium with discrete telomeres (figs. 24 and 26). Subcosta free throughout 15
15. Head transverse, without macrochaetae. 4 spermathecae (♀) Eurychoromyiidae
- Head usually with macrochaetae (except in *Celyphus* and its

- relatives, which are readily recognizable by their enlarged scutellum). 3 spermathecae (♀) Lauxaniidae
16. Male postabdomen (figs. 43, 46, 48 and 51) fully symmetrical, except in *Somatia* (Periscelididae); 6th tergum usually as long as preceding terga (except Nothybidae); symmetrical 6th sternum always retained; usually single dorsal sclerite between 6th segment and hypopygium (lost only in some Psilidae). Post-
verticals, when well developed, divergent
. (Nothyboidea) . . . 17
- Male postabdomen usually asymmetrical, with 6th and 7th sterna more strongly developed on left side where latter is linked to large 8th sternum (inverted); discrete symmetrical 6th sternum present only in Heteromyzidae and Micropezoina (figs. 56 and 71); in groups in which this asymmetrical arrangement of sterna is no longer apparent due to loss or fusion of sclerites, last symmetrical sternum in ventral position is 5th sternum. 6th tergum (♂) variably developed (in some groups reduced or lost); 7th tergum reduced to lateroventral vestige on right side or lost (Muscoidea) . . . 20
17. Ejaculatory apodeme (♂) reduced or lost. Spermathecae (♀) not sclerotized, represented by branched tubes. Female postabdomen elongate, forming retractile ovipositor. Subcosta cut off distally, connected with wing margin by hyaline stria Psilidae
- Ejaculatory apodeme (♂) and spermathecae (♀) well developed. Female postabdomen not elongate 18
18. 7th abdominal spiracles (♂) within pregenital sclerite (fig. 46);

aedeagus slender and ribbon-like throughout, without complex distal section (fig. 47). 7th abdominal tergum and sternum fused in female. Anal vein short, cut off apically. Postverticals usually well developed (except *Somatia*)

. Periscelididae

- 7th abdominal spiracles (♂) in membrane (Nothybidae) (fig. 43) or lost (Teratomyzidae) (fig. 51); if aedeagus partly ribbon-like (Nothybidae), it bears complex distal section (fig. 44).

7th abdominal tergum and sternum (♀) discrete or fused. Anal vein long, close to wing margin. Postverticals reduced or lost 19

19. Subcosta faded or fused with r_1 distally; costa broken; posterior cross-vein (m-m) displaced towards wing base. 1 *ors*. 7th abdominal spiracles lost in both sexes

. Teratomyzidae

- Subcosta distinct to wing margin; costa unbroken; posterior cross-vein remote from wing base. 2 *ors*. 7th abdominal spiracles present in both sexes Nothybidae

20. Abdomen with petiolate appearance, with basal segments elongate but distal segments short and wide (fig. 77). Postverticals absent; only one vertical bristle and at most one *ors* present. 6th sternum (♂) well developed only in *Centrioncus* (Diopsidae, fig. 77); in other groups reduced to pair of fragments . .

. (Diopsioinea) . . . 21

- Abdomen not petiolate; if markedly elongate (e.g. Micropezoinae, Megamerinidae), elongation more uniform, affecting both basal and distal segments 22

21. Front femora thickened and armed with ventral tubercles.
 Lower cross-vein lost. Scutellum with pair of spines . . .
 Diopsidae
- Hind femora thickened. Lower cross-vein usually present.
 Scutellum without spines Syringogastridae
22. Periandrium (♂) elongate; aedeagus borne on long basal cone;
 6th tergum as long as preceding terga; 6th sternum subtriangular,
 more or less symmetrical (enlarged in some Micropezidae) (figs.
 71-73). 7th tergum and sternum (♀) lengthened to form more or
 less closed ovipositor sheath (Micropezoinea) . . . 23
- Male postabdomen and genitalia not as above 25
23. Lower cross-vein lost; subcosta not distinct to wing margin;
 costa broken. Ocellar bristles well developed
 Cypselosomatidae
- Lower cross-vein usually present; subcosta distinct to wing
 margin; costa broken or unbroken. Ocellar bristles reduced or
 lost 24
24. 2nd antennal article with fingerlike process on inner side;
 arista apical or subapical. Front legs long
 Neriidae
- 2nd antennal article without fingerlike process; arista medial
 to subbasal. Front legs relatively short and weak
 Micropezidae
25. 2nd antennal article with suture; *ori* usually present. Pre-
 abdominal spiracles within terga (except Glossinidae). 7th
 left spiracle (♂) within 7th sternum or synsternum (7+8)
 (except in *Haematobia*, Muscidae). Inner mouth-opening with

- hyoid (except in Stomoxyinae, Muscidae)
- (Calyptratae, part) 26
- 2nd antennal article usually without suture (except in *Mormotomyia*, some Megamerinidae and some Tephritidae). Pre-abdominal spiracles usually in membrane. Hyoid absent 31
26. Three radial branches and m_{1+2} crowded on fore-margin of wing. Mouthparts piercing (adapted for blood sucking). 6th to 8th sterna (♂) fused to form composite pregenital sclerite (fig. 67); 6th tergum as long as 5th tergum Glossinidae
- Veins usually not crowded on fore-margin of wing; or, if somewhat crowded (*Oestrus*, *Gasterophilus* and relatives), mouthparts reduced. 6th tergum (♂) shorter than 5th tergum, in some groups much reduced or lost; 6th sternum usually discrete (except Fanniidae) 27
27. Hypopleuron with row of outstanding bristles, except in *Gasterophilus* which may be recognized by its reduced mouthparts Tachinidae (*sensu lato*)
- Hypopleuron without outstanding bristles, at most with fine pubescence (*Eginia*) 28
28. Lower fold of squama ("thoracic squama") consisting of narrow strip. Frons not sexually dimorphic (eyes widely separated in male). Aedeagus (♂) swung through wide arc against aedeagal apodeme to anteriorly directed rest position, with well-developed epiphallus; articulated pregonites present (fig. 60) Scatophagidae (limits of family not clarified)

- Lower fold of squama expanded (except Fucelliinae, in which aedeagus is posteriorly directed at rest and epiphallus lost).
Frons sexually dimorphic (narrower in male) in many groups 29
- 29. 6th to 8th sterna (♂) fused to form symmetrical pregenital sclerite, within which both 6th and 7th pairs of spiracles are situated (fig. 63); aedeagus small (often membranous); hypandrium without articulated pregonites Fanniidae
- Male postabdomen not as above; 6th sternum retained as discrete asymmetrical sclerite; articulated pregonites usually present (except in some Muscidae) 30
- 30. 6th and 7th abdominal spiracles usually lost in female (at most with 6th pair retained in *Acanthiptera*). Processus longi (♂) absent. Anal vein not distinct to wing margin Muscidae
- Anal vein distinct to wing margin Anthomyiidae
(limits of family not clarified)
- 31. 7th sternum (♂) and 7th tergum vestige fused as complete ring of sclerotization; 6th tergum as long as 5th tergum; periandrium divided into two halves (figs. 74-76) Australimyziidae
- 7th sternum and tergum (♂) not thus fused, except in *Helcomyza* (Dryomyzidae) in which 6th tergum reduced; periandrium entire, except in *Aphaniosoma* (Chyromyidae) 32
- 32. 6th sternum (♂) large and discrete, symmetrical or somewhat

- asymmetrical (if asymmetrical, 6th tergum as long as 5th tergum); epiphallus well developed (figs. 54-58). 7th abdominal spiracles lost in both sexes. Frons sexually dimorphic (narrower in male) in many species (Tanypezoinea) . . . 33
- 6th sternum (♂) strongly asymmetrical (more strongly developed on left side), except when reduced or fused with succeeding sterna as composite pregenital sclerite. Frons not sexually dimorphic, except in *Neomaorina* (Tephritidae family-group) 34
33. 6th sternum (♂) asymmetrical (extending towards 7th sternum on left side); telomeres fused with periandrium; aedeagal apodeme linked to hypandrium by ventral process or pair of ventral processes (figs. 54-55). Postverticals divergent Tanypezidae
- 6th sternum (♂) symmetrical; telomeres discrete; aedeagal apodeme free from hypandrium (figs. 56-58). Postverticals convergent Heteromyzidae
34. Aedeagus (♂) flexible, coiled at rest, extended by pressure of body fluid (often very long and distinctly pubescent); but reduced in Milichiidae, Chloropidae and some Conopidae (without distinct sclerites beyond basal phallopore) (figs. 122-146). Female usually with retractile ovipositor formed by elongation of 7th and 8th abdominal segments (except in some genera of Chloropidae and Tethinidae) (Tephritoinea) . . . 35

- Aedeagus more or less rigid, not coiled at rest, with its walls usually supported by well differentiated sclerites (exceptionally with coiled distal section in some Agromyzidae or coiled basal section in some Clusiidae); without extensive pubescence except in Dryomyzidae 48
35. Wings vestigial; whole body densely clothed with ochraceous pubescence; eyes very small, ocelli lost. 7th abdominal spiracles lost in both sexes. 6th tergum (♂) large; hypandrium modified to form pubescent trough-like structure (fig. 126) Mormotomyiidae
- Not as above 36
36. 2nd antennal article elongate; haustellum elongate. 7th and 8th sterna (♂) fully fused (fig. 139), forming more or less symmetrical pregenital sclerite with which 6th sternum is joined on both sides; both 6th and 7th abdominal spiracles symmetrically situated within this pregenital sclerite (except in the highly modified *Stylogaster* in which there are no clearly defined sclerites between 5th segment and hypopygium). Ovipositor (♂) (segments 7 and following) usually directed obliquely in relation to longitudinal axis of abdomen (except *Stylogaster*) Conopidae
- 2nd antennal article and haustellum not both elongate in combination (one or other elongate in few groups, such as Milichiidae and some Tephritidae); postabdominal structure not as stated above 37

37. 7th abdominal segment (♀) extremely long (at least twice as long as 6th segment); 8th segment extremely long, retractile within 7th segment; female cerci more or less fused. Spermathecae (♀) well developed. 8th sternum (♂) asymmetrically developed on left side of abdomen: aedeagus usually extremely long and coiled (but membranous in some groups of Piophilidae, and somewhat shortened in *Heloparia*) (figs. 140-146)
 (Tephritidae family-group). 38
- Elongation of 7th and 8th abdominal segments (♀) less extreme; female cerci more or less discrete except in Carnidae (in which spermathecae reduced). 8th sternum (♂) not strongly asymmetrical, in some groups fused with preceding sclerites or reduced (Milichiidae) 41
39. 6th tergum (♂) represented by two fragments, one of which lies above 6th left spiracle on left side (fig. 140). 7th abdominal spiracles lost in both sexes
 Eurygnathomyiidae
- 6th tergum (♂) represented at most by narrow band (*Heloparia*) or lateroventral fragment on right side. 6th and 7th abdominal spiracles retained in all females, but lost in most males (except Richardiidae) 39
39. 6th and 7th abdominal spiracles (♂) retained on left or on both sides (fig. 142). 7th tergum and sternum (♀) fused as completely sclerotized oviscape. Vein r_1 thickened where subcosta ends, then forming a short convex bow Richardiidae
- 6th and 7th abdominal spiracles (♂) lost on both sides
 40

40. 7th tergum and sternum (♀) fused as completely sclerotized
oviscape. Postgonites absent (♂)
.Tephritidae (*sensu lato*)
- 7th tergum and sternum (♀) discrete, becoming attenuated to
pairs of thin strips posteriorly. Large postgonites present
(♂) Piophilidae (*sensu lato*)

Note. Certain southern hemisphere genera previously classified in the
"Pallopteridae" (e.g. *Heloparia*, *Aenigmatomyia* and *Neomaorina*) are not
included in the above dichotomy.

41. Aedeagus (♂) reduced (figs. 135 and 136), virtually membranous
beyond basal phallopore (at most with weak traces of pubescence).
Spermathecae (♀) rudimentary 42
- Aedeagus (♂) elongate; or, if rather short (as in Odiniidae),
still conspicuously pubescent 43
42. Male postabdomen symmetrical (fig. 133), with only single
narrow dorsal sclerite (in *Desmometopa* reduced to pair of lateral
strips) between 5th segment and hypopygium. Anal cell and lower
cross-vein retained. Ocellar plate not enlarged
. Milichiidae
- Male postabdomen variable in structure, with asymmetrical 6th
and 7th sterna clearly delimited in some genera (e.g. *Lasiopleura*,
fig. 137), but lost in others (e.g. *Chlorops*, *Meromyza*) in which
postabdomen appears more or less symmetrical. Anal cell and lower
cross-vein lost. Ocellar plate enlarged
. Chloropidae
43. Male postabdomen fully symmetrical (fig. 129); 6th tergum fused
with 8th sternum; 6th and 7th sterna lost. Hypandrium (♂) much
shorter than aedeagal apodeme. Postverticals convergent.

- Spermathecae (♀) well developed Tethinidae
- Male postabdomen usually strongly asymmetrical (with 6th and 7th sterna clearly delimited); if almost symmetrical due to fusion of sterna (Acartophthalmidae), 6th tergum lost but 6th sternum retained 44
44. 7th and 8th sterna (♂) fused, forming almost symmetrical pre-genital sclerite with which 6th sternum is joined on both sides (fig. 132). Sclerotized spermathecae absent (♀). Costal break shortly beyond humeral cross vein. Postverticals divergent Acartophthalmidae
- Male postabdomen not as above. Costal break at end of subcosta or r_1 45
45. 7th tergum vestige (♂) on centre-line of venter (fig. 134). Sclerotized spermathecae absent (♀); female cerci fused to form stylus-like structure Carnidae
- 7th tergum vestige (♂) on right side of venter (Chiropteromyzidae, fig. 122) or lost (Cnemospathidae, Odiniidae). Sclerotized spermathecae present (♀) 46
46. 7th abdominal spiracles lost in both sexes. Periandrium (♂) with pair of lateral notches on anterior margin; telomeres not discrete; aedeagal apodeme short (fig. 127). Postverticals convergent Cnemospathidae
- 7th abdominal spiracles retained. Periandrium (♂) without lateral notches, with or without discrete telomeres; aedeagal apodeme long and rod-like 47
47. 7th tergum vestige (♂) lost; hypandrium long and narrow anteriorly; aedeagus rather short (fig. 128); ejaculatory apodeme lost.

- Postverticals divergent; 3 *ors* present
- Odiniidae
- 7th tergum vestige (♂) present; hypandrium shorter; aedeagus
very long (figs. 122-123); ejaculatory apodeme present. Post-
verticals convergent; 2 *ors* present
- Chiropteromyzidae
48. Male postabdomen fully symmetrical (fig. 120); 5th sternum last
ventral sclerite before hypopygium; 6th tergum last large dorsal
sclerite before hypopygium (with inverted 8th sternum represented
at most by narrow band). Female with piercing ovipositor; 7th
abdominal segment forming conical ovipositor sheath; 8th segment
bearing numerous anteriorly directed denticles; proctiger elongate.
One or more pairs of inwardly directed *ori* present; divergent
postverticals usually present (except *Penetagromyza*)
- Agromyzidae
- Male and female postabdomen not as above 49
49. 2nd antennal article with angular projection on its outer side.
6th tergum (♂) well developed (at least half as long as 5th tergum).
At least three pairs of orbital bristles present, usually including
pair of inwardly directed *ori*; postverticals, when present,
divergent Clusiidae
- 2nd antennal article without such angular projection 50
50. Metatarsus of hind legs short and thick. 6th tergum (♂) lost;
6th and 7th left spiracles both within 6th sternum; 7th right
spiracle lost (fig. 113) Sphaeroceridae
- Metatarsus of hind legs slender (similar to metatarsi of front two
pairs of legs) 51

51. Costa unbroken 52
- Costa broken near end of subcosta or r_1
- (Anthomyzoinea, part) . . 62
52. Anal cell and lower cross-vein lost. 7th abdominal spiracles
lost in both sexes. Postverticals reduced
- Asteiidae
- Anal cell and lower cross-vein present
- (Sciomyzoinea) . . . 53
53. Ocellar and postvertical bristles lost. Hind femora thickened
and armed with spines. Abdominal segments elongate, except
reduced male 6th and 7th segments (fig. 97)
- Megamerinidae
- Ocellar bristles present 54
54. Metastigmatal bristles present (posterior to metathoracic
spiracles) 55
- Metastigmatal bristles absent; metathoracic spiracles with
fine pubescence only 56
55. Hypandrial arms (σ) fused above base of aedeagus, where they
bear conspicuous upcurved process (fig. 94); aedeagus with
long membranous distal area; telomeres discrete
- Ropalomeridae
- Hypandrial arms (σ) not bearing upcurved process; aedeagus with
distal sclerotization; telomeres fused with periandrium . . .
- Sepsidae
56. Subcostal cell infuscated. Postverticals reduced
- Cremifaniidae
- Subcostal cell not infuscated. Postverticals well developed
. 57

57. Male with thumbnail-like apical ventral processes on at least front and hind metatarsi; aedeagus extensively pubescent (fig. 88) Dryomyzidae
- Metatarsi without such processes; aedeagus without extensive pubescence 58
58. 6th tergum (♂) well developed, symmetrical, about half as long as 5th tergum (fig. 82)
- *Heterocheila* (? Coelopidae)
- 6th tergum (♂) further reduced or lost, in some groups asymmetrically developed on right side 59
59. 7th and 8th tergum vestiges present (♂); 6th tergum asymmetrically reduced, developed mainly on right side (figs. 81 and 85) 60
- 7th and 8th tergum vestiges lost (♂); 6th tergum reduced to symmetrical narrow band or lost 61
60. Postverticals convergent. 6th and 7th left spiracles (♂) in membrane Coelopidae
- Postverticals divergent. 6th and 7th left spiracles (♂) within 6th and 7th sterna (fig. 86) Phaeomyiidae
61. Postverticals parallel or convergent. Aedeagus (♂) bilobed distally (fig. 93). 3 spermathecae (♀) Helosciomyzidae
- Postverticals divergent. Aedeagus (♂) variously modified. 2 spermathecae (♀) Sciomyzidae
62. Postverticals divergent; only one pair of vertical bristles present. Aedeagus (♂) slender
- *Stenomicro* (? Anthomyzidae)
- Postverticals, if well developed, convergent; two pairs of vertical bristles retained 63

63. Ocellar bristles reduced; postverticals lost. 2 *ors*, of which anterior pair directed inwards. Aedeagus (♂) short, with very complex sclerotization (fig. 116) Aulacigastridae
- Ocellar bristles well developed 64
64. Male postabdomen symmetrical, sometimes with much reduced sclerotization (*Aphaniosoma*); 6th tergum with lateroventral extensions, entire in *Chyromya* (fig. 115) but divided in *Aphaniosoma*; 6th and 7th sterna lost; aedeagus with expanded complex distal area (fig. 117) Chyromyidae
- Male postabdomen usually obviously asymmetrical (except in some Rhinotoridae); 6th tergum, when present, without lateroventral extensions 65
65. Postverticals reduced or lost; only 1 *ors* present. Aedeagus (♂) with very complex sclerotization (fig. 109); telomeres not differentiated from periandrium; 6th tergum reduced to narrow band or lost. 7th abdominal spiracles lost in both sexes Opomyzidae
- Not as above. Postverticals usually present (except in some Rhinotoridae and Anthomyzidae) 66
66. Aedeagus (♂) with expanded medial area from which arises slender distal section (fig. 104); ejaculatory apodeme reduced Anthomyzidae
- Aedeagus (♂) not as above; ejaculatory apodeme well developed 67
67. Aedeagus (♂) not swung through wide arc against aedeagal apodeme; 5th sternum (♂) usually divided (fig. 106); male cerci small.

Femora (especially of front legs) somewhat thickened, usually
with spines on their ventral surface

. Rhinotoridae

- Aedeagus (♂) swung through wide arc against aedeagal apodeme
to anteriorly directed rest position; 5th sternum (♂) entire . . 68

- 68. Slender epiphallus present (♂); 7th tergum vestige present (♂);
aedeagal apodeme free from hypandrium (figs. 110-111). 7th
abdominal spiracles retained in both sexes

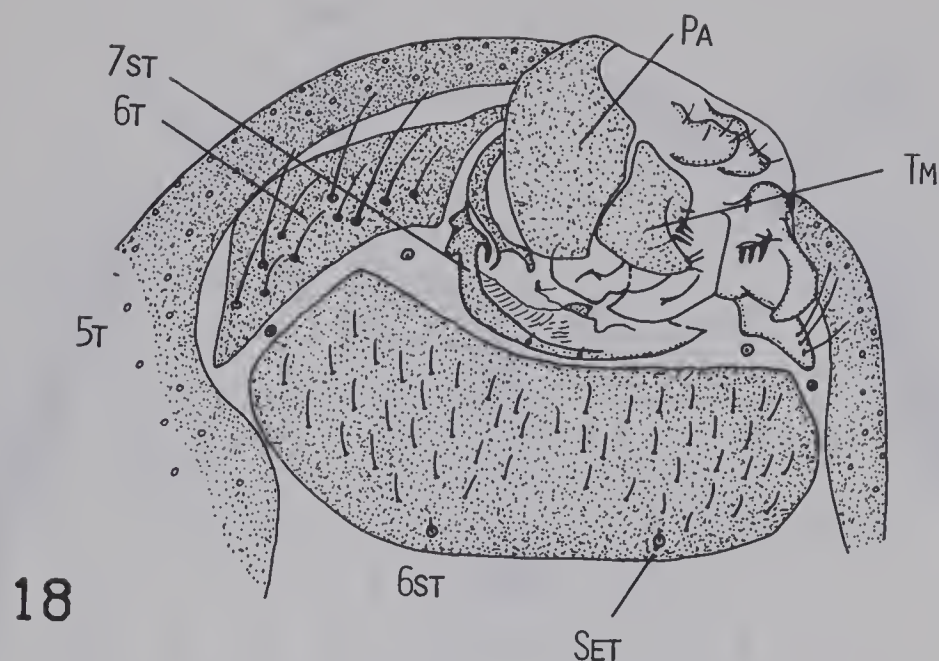
. Borboropsidae

- Epiphallus (♂) short or absent; 7th tergum vestige usually absent
(except *Anorostoma* and *Orbellia*, Heleomyzidae) 69

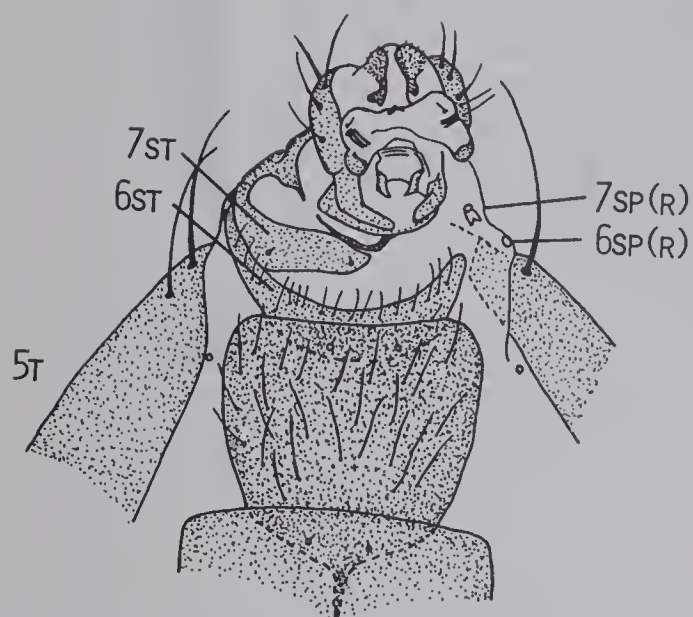
- 69. 7th abdominal spiracles lost in both sexes. Aedeagal apodeme
(♂) free from hypandrium (fig. 107)

. Trixoscelididae
(limits of family not clarified)

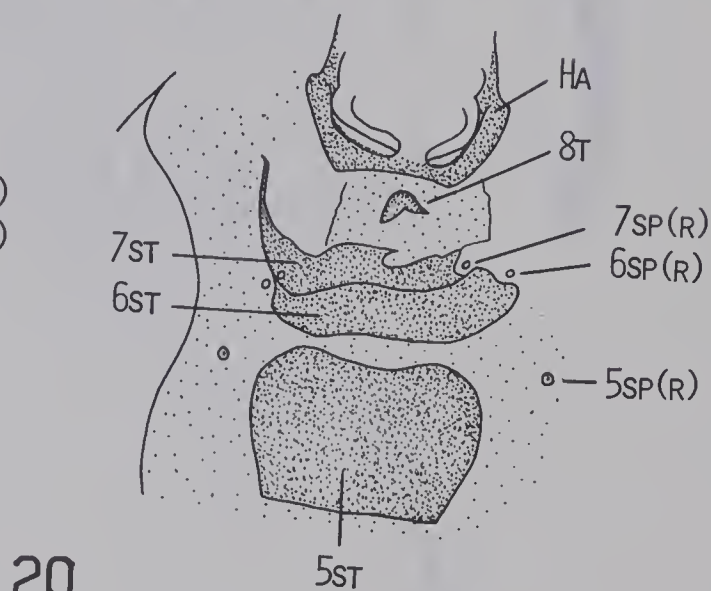
- 7th abdominal spiracles usually retained (except *Allophylopsis*).
Aedeagal apodeme (♂) linked to hypandrium by single or paired
ventral processes Heleomyzidae
(limits of family not clarified)



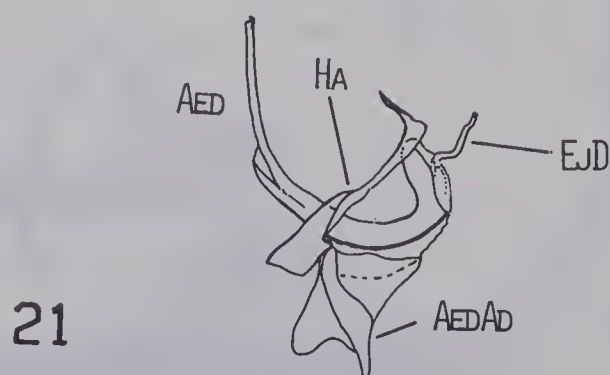
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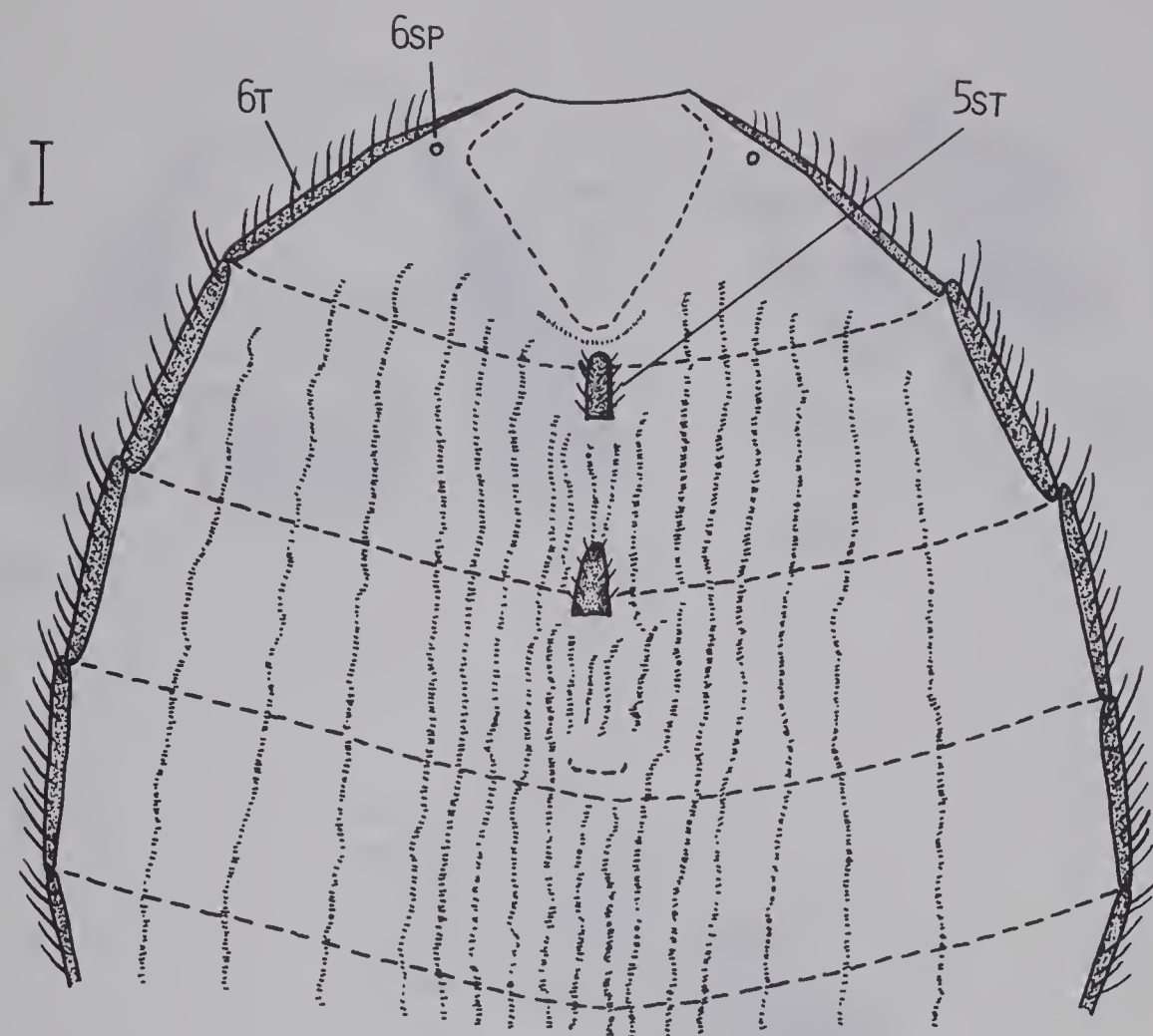


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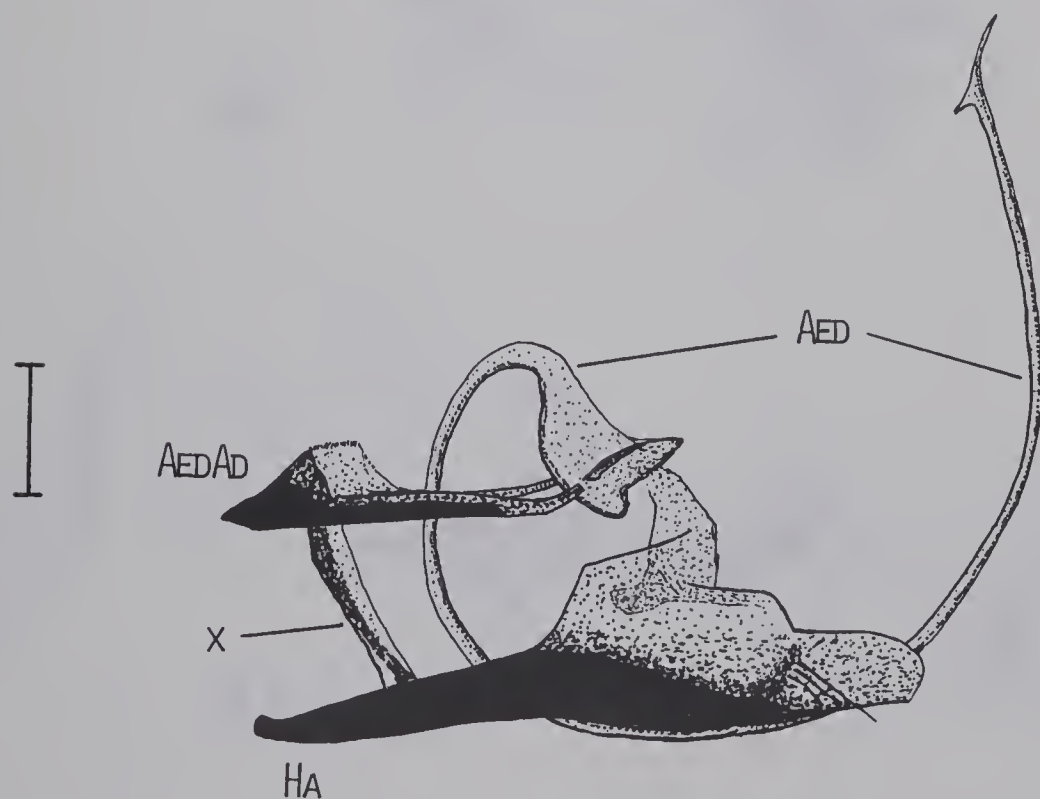


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Figs. 18 - 21. 18. *Dasiops relictus* McAlpine (Lonchaeidae), postabdomen (♂) in ventral view (after J. F. McAlpine 1962b). 19. *Protearomyia obscura* (Walker) (Lonchaeidae), postabdomen (♂) in ventral view (after J. F. McAlpine 1962b). 20. *Lonchaea subpolita* Malloch (Lonchaeidae), ventral postabdominal sclerites (♂) (after J. F. McAlpine 1962b). 21. *Lamprolonchaea aurea* (Macquart) (Lonchaeidae), aedeagus, hypandrium and associated structures (♂) in lateral view (after J. F. McAlpine 1962b).



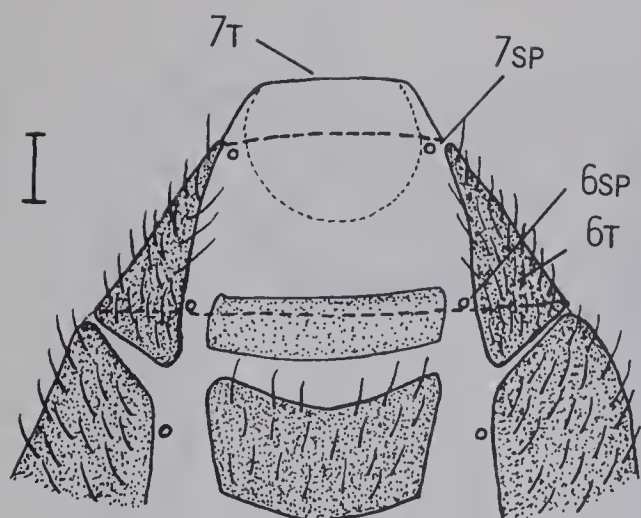
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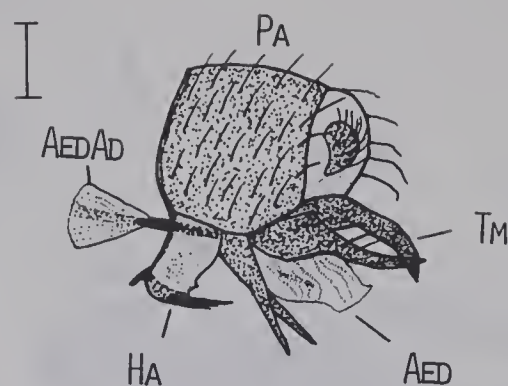
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Figs. 22 - 23. 22. *Cryptochetum nipponense* Tokunaga (Cryptochetidae), abdomen (♂) (part) in ventral view (with hypopygium removed). 23. *Cryptochetum nipponense* Tokunaga, aedeagus, hypandrium and associated structures (♂) in lateral view.

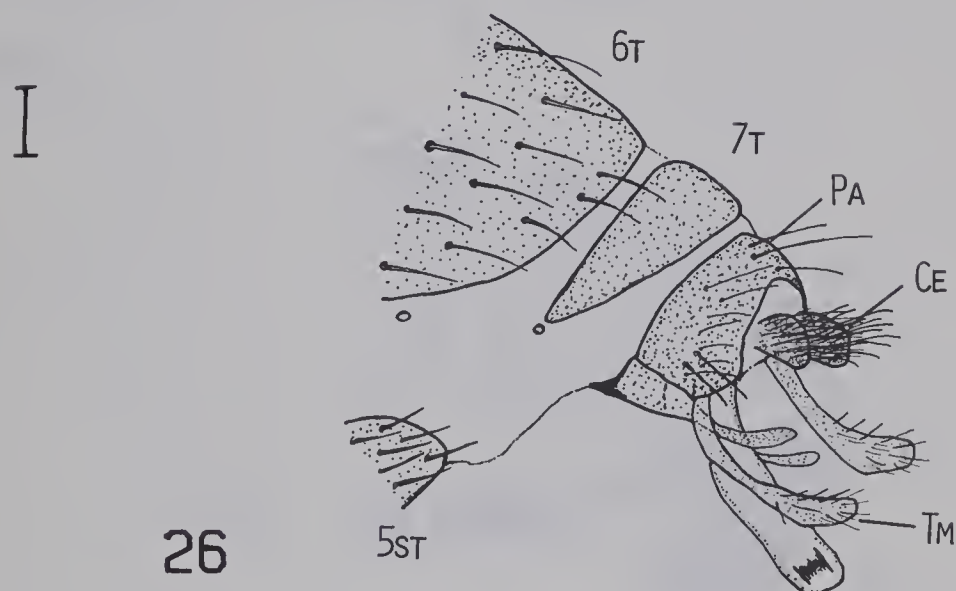
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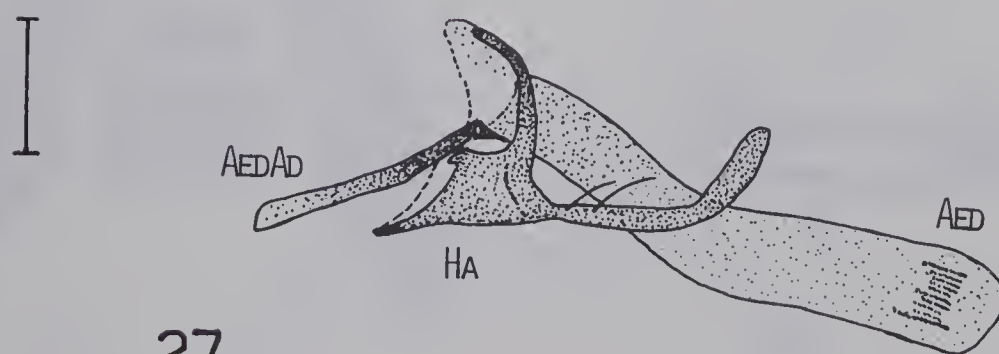
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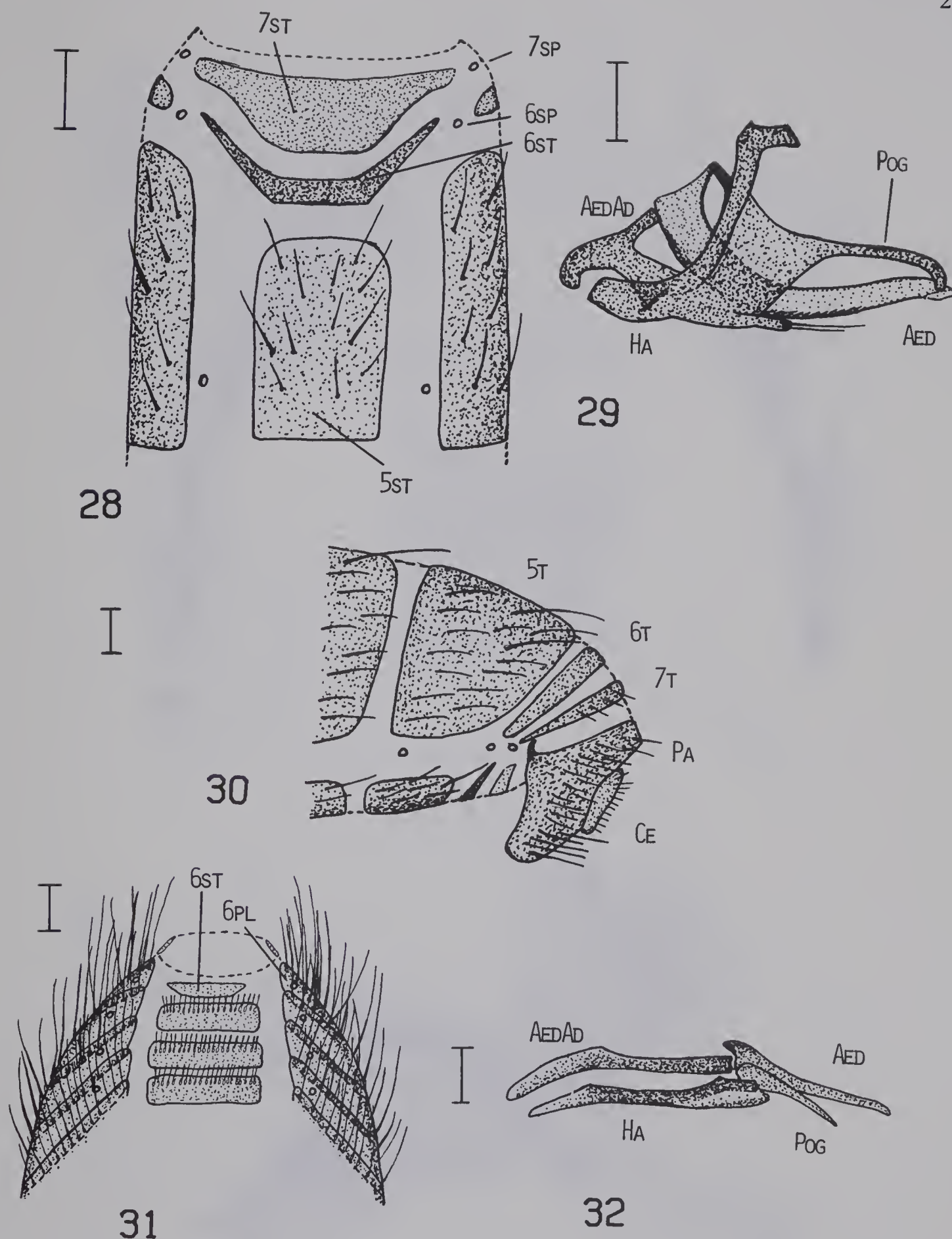
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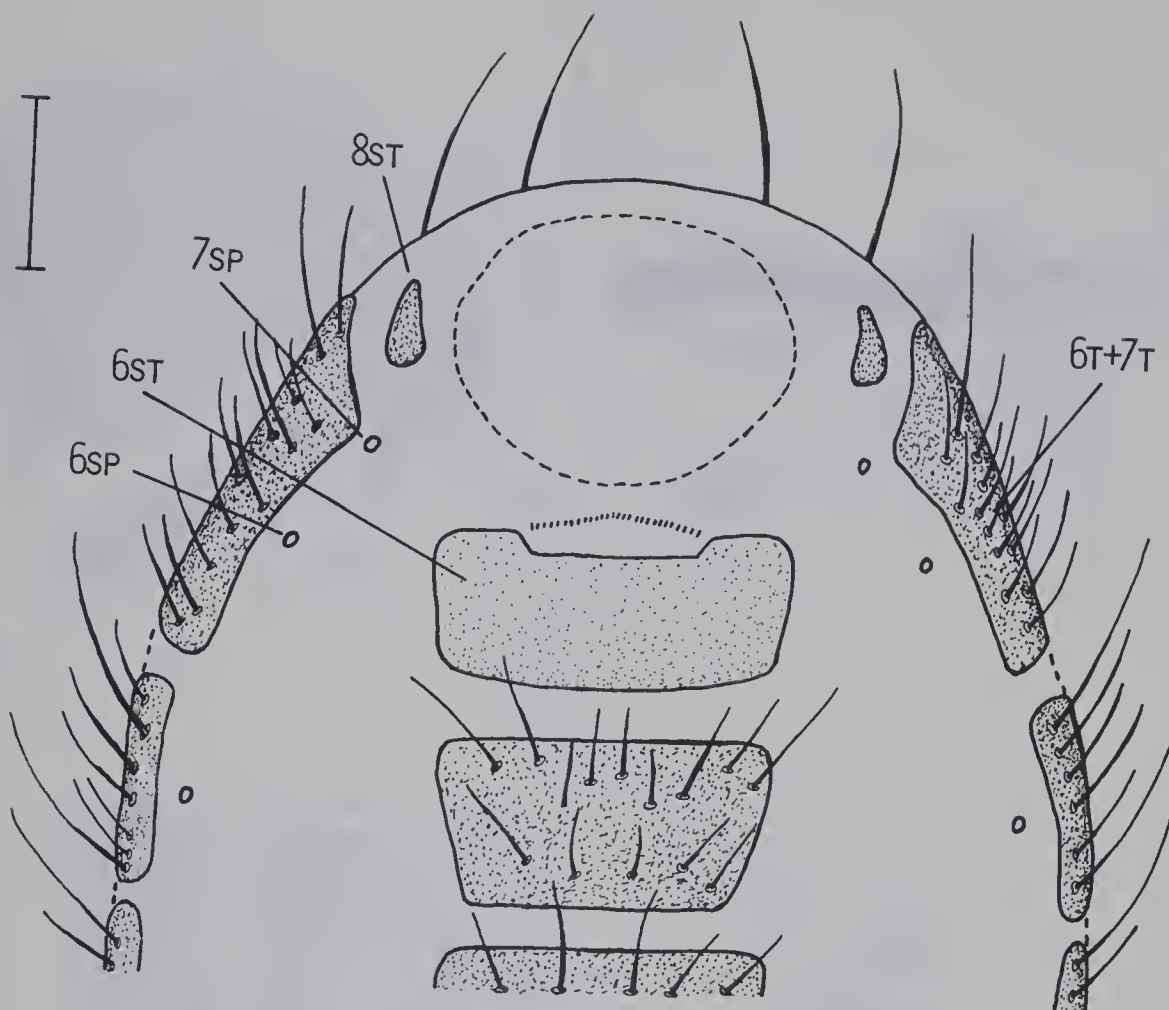
Figs. 24 - 27. 24. *Lauxania cylindricornis* (F.) (Lauxaniidae), postabdomen (♂) in ventral view (with hypopygium removed). 25. *Lauxania cylindricornis* (F.), hypopygium (♂) in lateral view. 26. *Camptoprosopella borealis* Shewell (Lauxaniidae), postabdomen (♂) in lateral view. 27. *Camptoprosopella borealis* Shewell, aedeagus, hypandrium and associated structures (♂) in lateral view.

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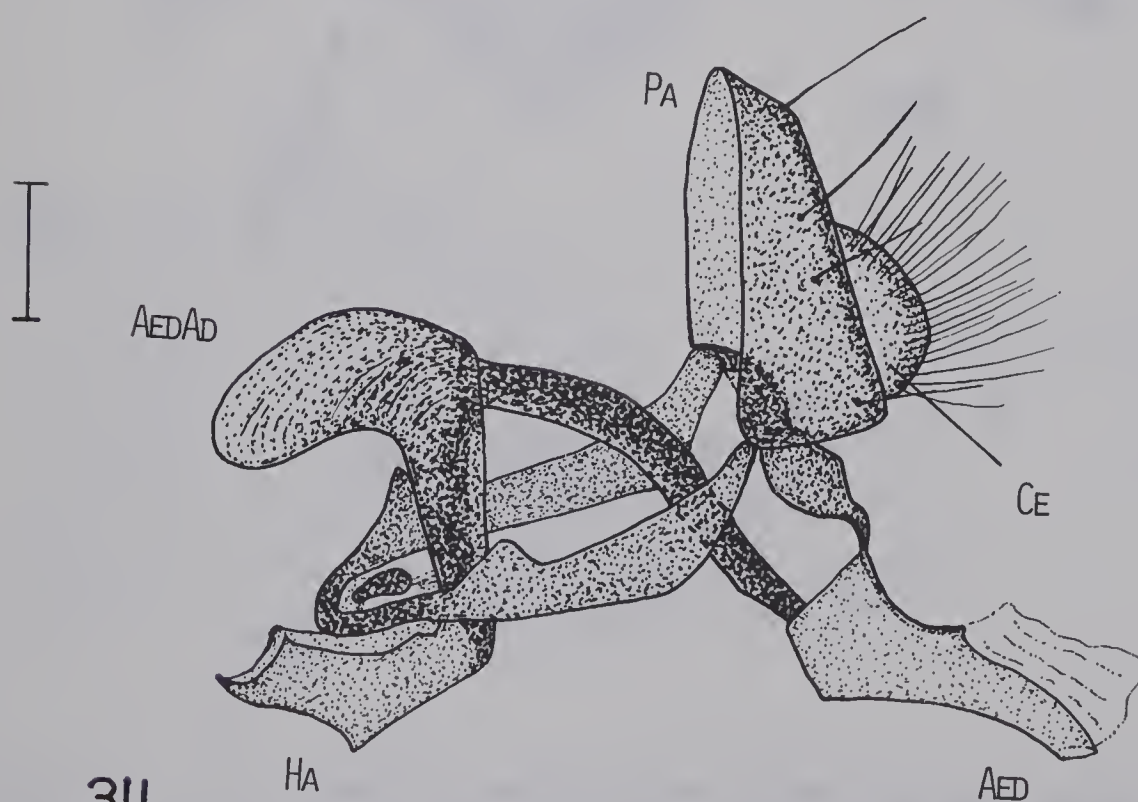


Figs. 28 - 32. 28. *Chamaemyia juncorum* (Fallén) (Chamaemyiidae), postabdomen (♂) in ventral view (with hypopygium removed). 29. *Chamaemyia juncorum* (Fallén), aedeagus, hypandrium and associated structures (♂) in lateral view. 30. *Chamaemyia juncorum* (Fallén), postabdomen (♂) in lateral view. 31. *Braula* sp. (Braulidae), abdomen (part) (♂) in ventral view (with hypopygium removed). 32. *Braula* sp., aedeagus, hypandrium and associated structures (♂) in lateral view.

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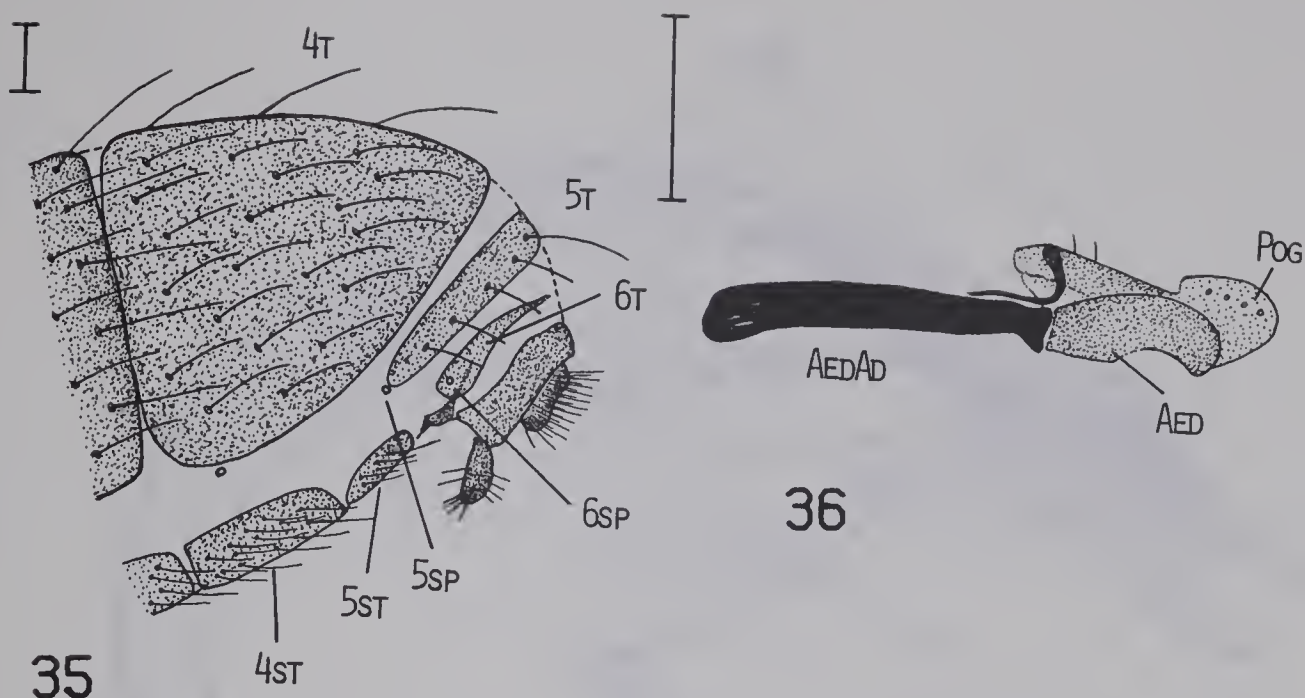
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Figs. 33 - 34. 33. *Drosophila* sp. cf. *melanogaster* Meigen (Drosophilidae), postabdomen (♂) in ventral view (with hypopygium removed). 34. *Amiota picta* (Coquillett) (Drosophilidae), hypopygium (♂) in lateral view.

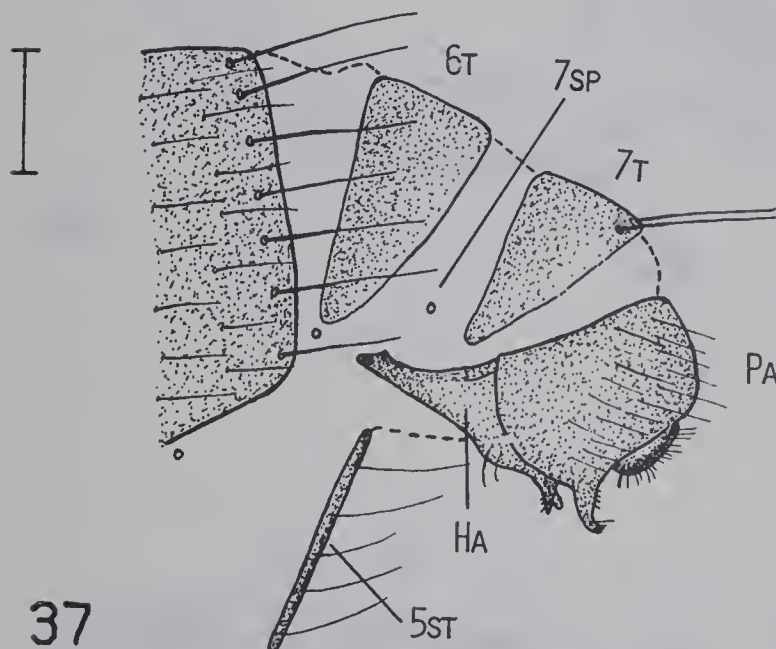
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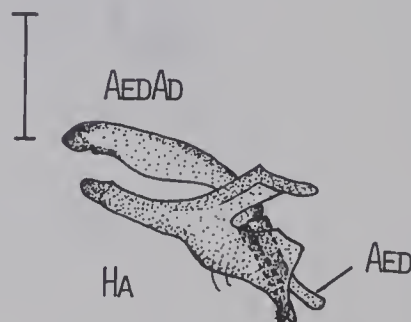
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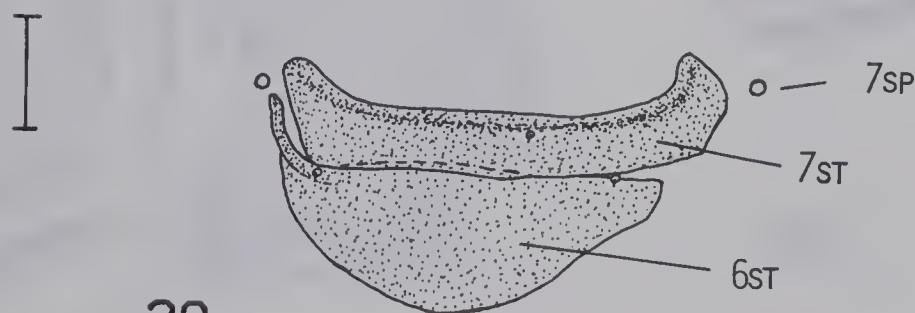
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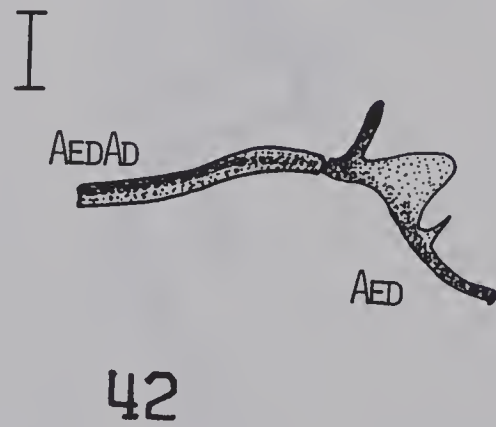
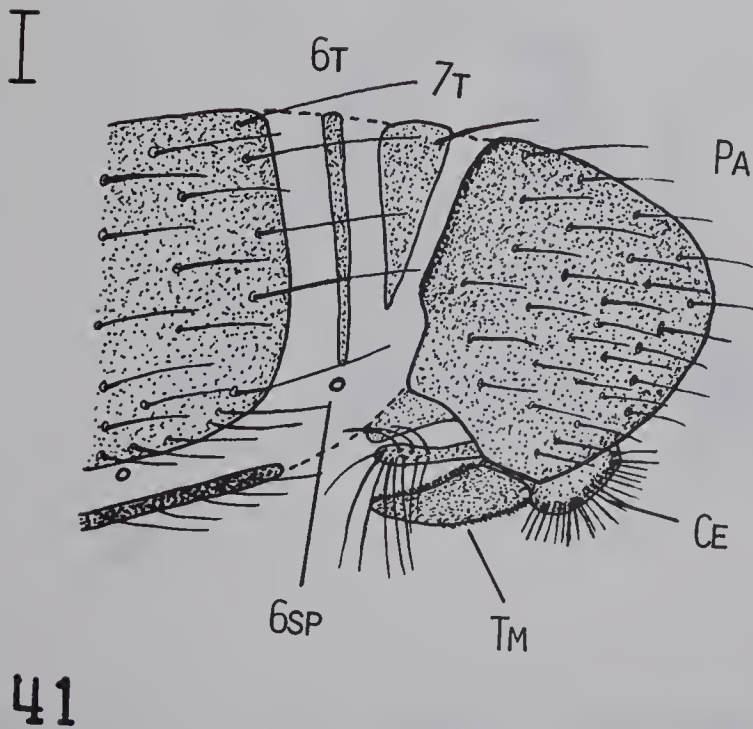
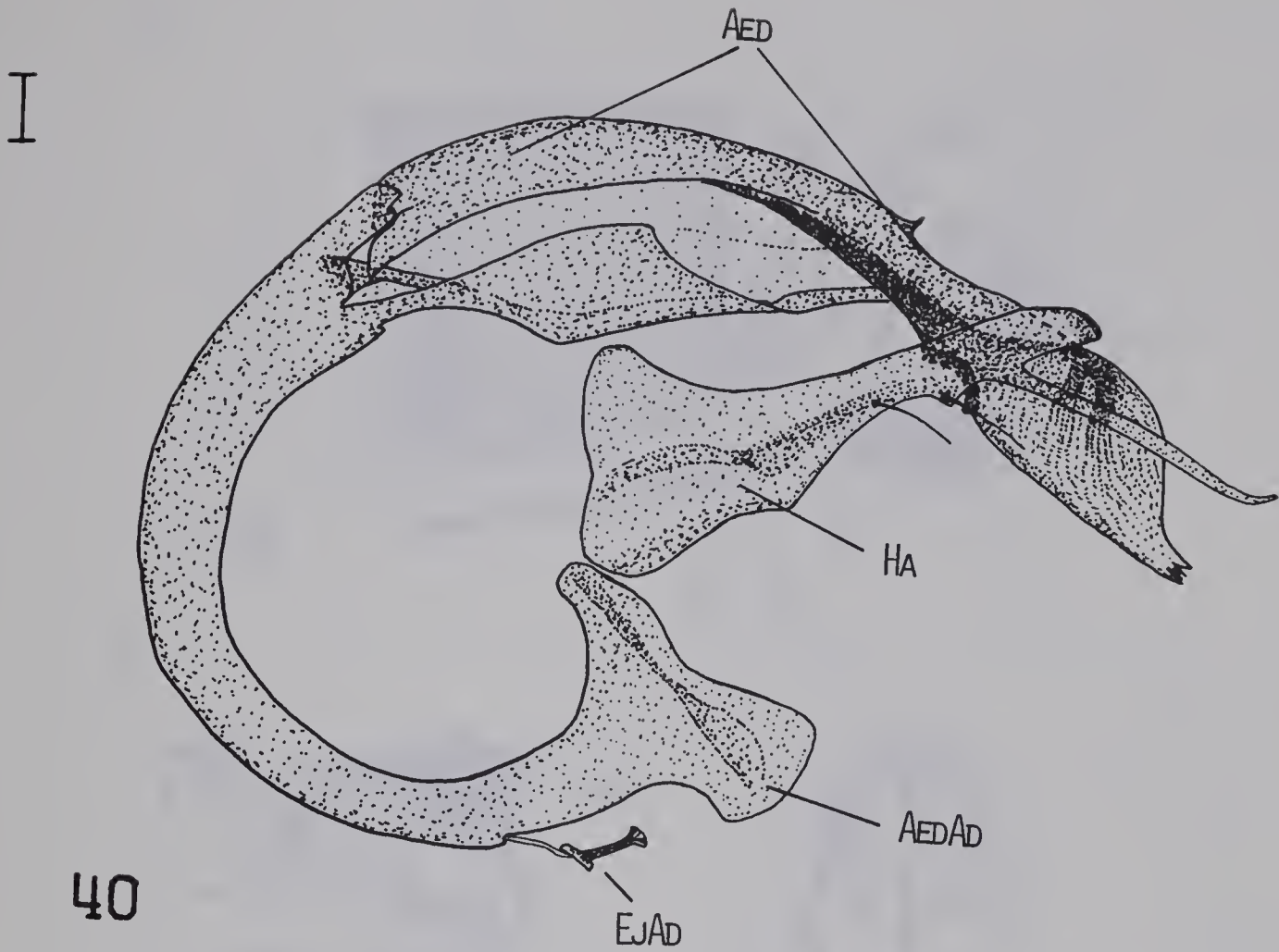
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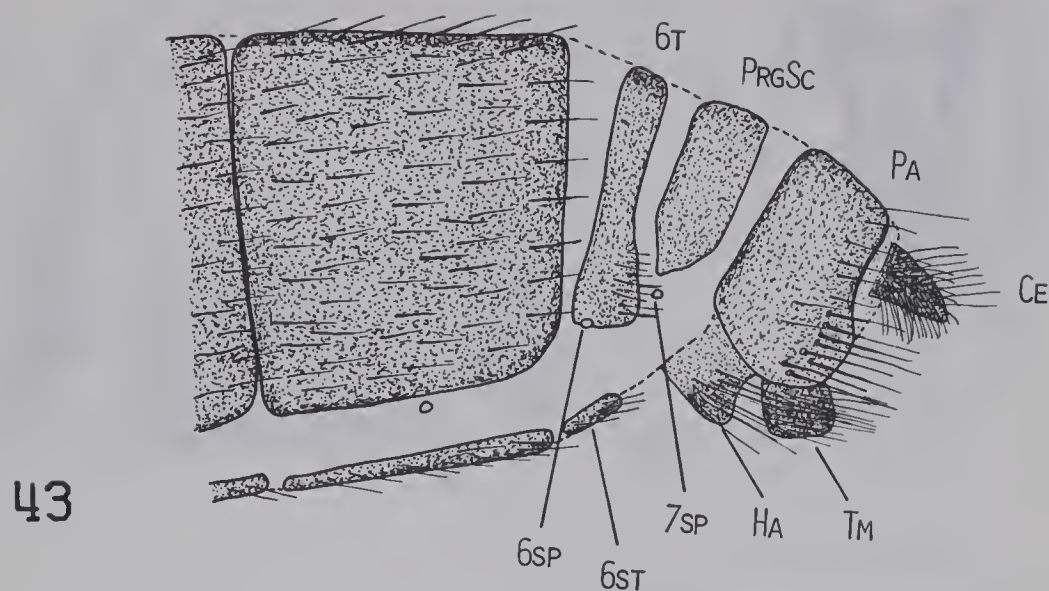
Figs. 35 - 39. 35. *Camilla atripes* Duda (Camillidae), abdomen (part) (♂) in lateral view. 36. *Camilla atripes* Duda, aedeagus and associated structures (♂) in lateral view (with the left postgonite removed). 37. *Campichoeta griseola* (Zetterstedt) (Campichoetidae), postabdomen (♂) in lateral view. 38. *Campichoeta griseola* (Zetterstedt), aedeagus, hypandrium and associated structures (♂) in lateral view. 39. *Curtonotum helvum* (Loew) (Curtonotidae), 6th and 7th sterna (♂) in posteroventral view.

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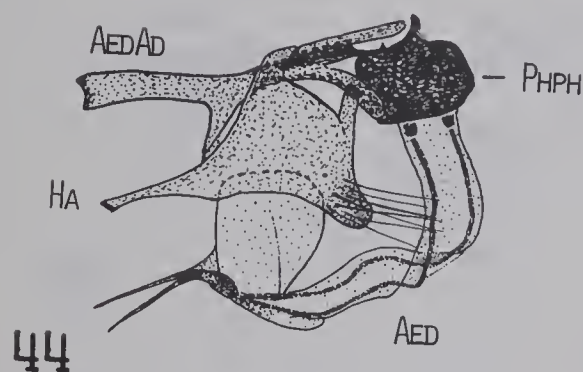


Figs. 40 - 42. 40. *Curtonotum helvum* (Loew) (Curtonotidae), aedeagus, hypandrium and associated structures (♂) in lateral view. 41. *Diastata vagans* Loew (Ephydriidae), postabdomen (♂) in lateral view. 42. *Diastata vagans* Loew, aedeagus and aedeagal apodeme (♂) in lateral view.

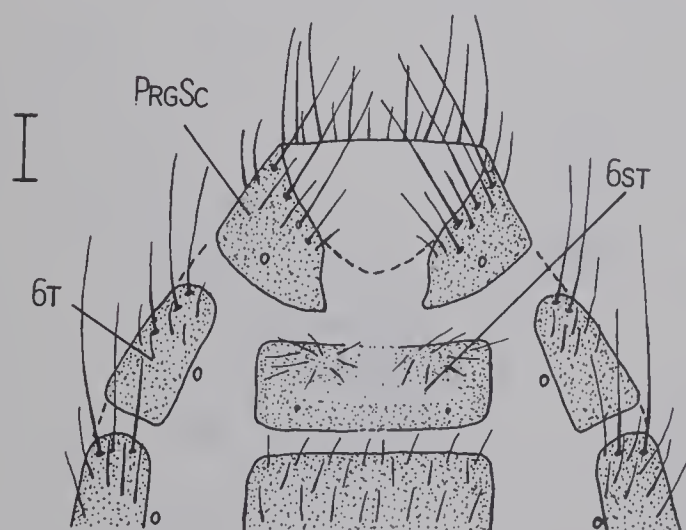
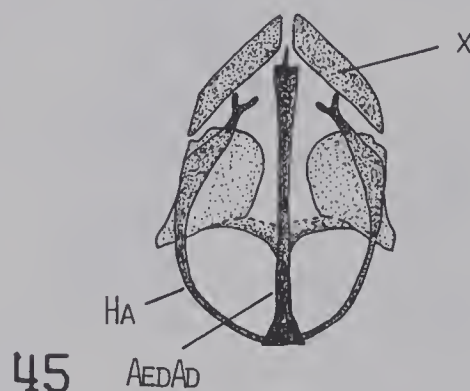
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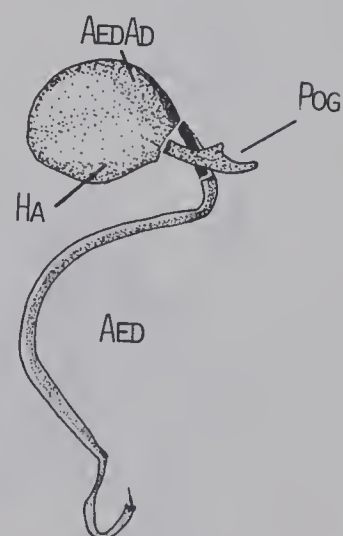
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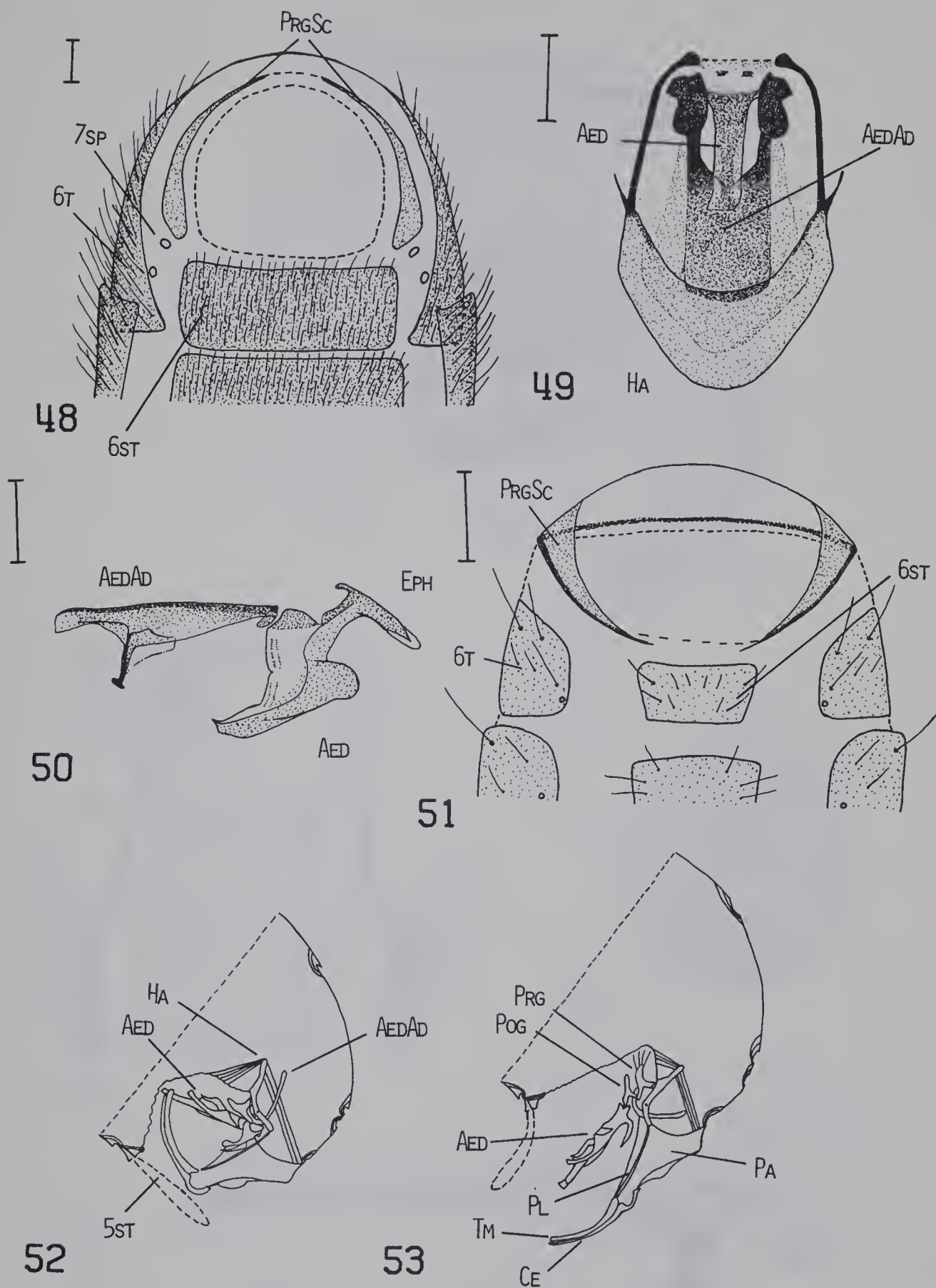


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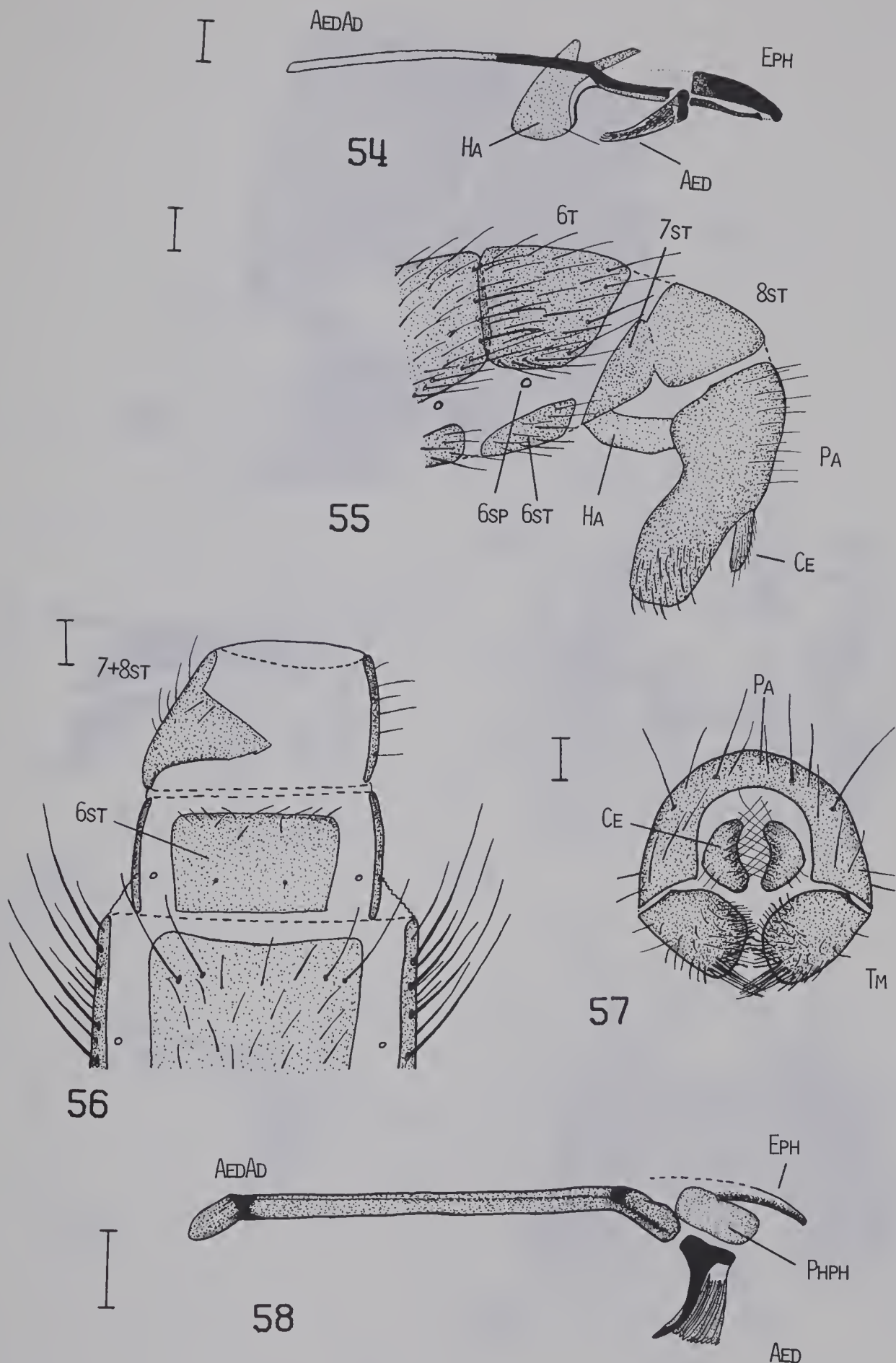
Figs. 43 - 47. 43. *Nothybus longithorax* Rondani (Nothybidae), post-abdomen (♂) in lateral view. 44. *Nothybus longithorax* Rondani, aedeagus, hypandrium and associated structures (♂) in lateral view. 45. *Nothybus longithorax* Rondani, hypandrium and aedeagal apodeme (♂) in dorsal view. 46. *Scutops maculipennis* Malloch (Periscelididae), postabdomen (♂) in ventral view (with hypopygium removed). 47. *Scutops maculipennis* Malloch, aedeagus, hypandrium and associated structures (♂) in lateral view.

(Scale lines 0.1 mm.)



Figs. 48 - 53. 48. *Loxocera cylindrica* Say (Psilidae), postabdomen (♂) in ventral view (with hypopygium removed). 49. *Psila rosae* (F.) (Psilidae), aedeagus, hypandrium and associated structures (♂) in ventral view. 50. *Teratomyza* sp. (Australia) (Teratomyzidae), aedeagus and associated structures (♂) in lateral view. 51. *Teratomyza* sp. (Australia), postabdomen (♂) in ventral view (with hypopygium removed). 52. *Calliphora erythrocephala* Meigen (Tachinidae s.l.), schematic representation of the male postabdomen in rest position (lateral view) (after Salzer 1968). 53. As the preceding, but in copulatory position (after Salzer 1968).

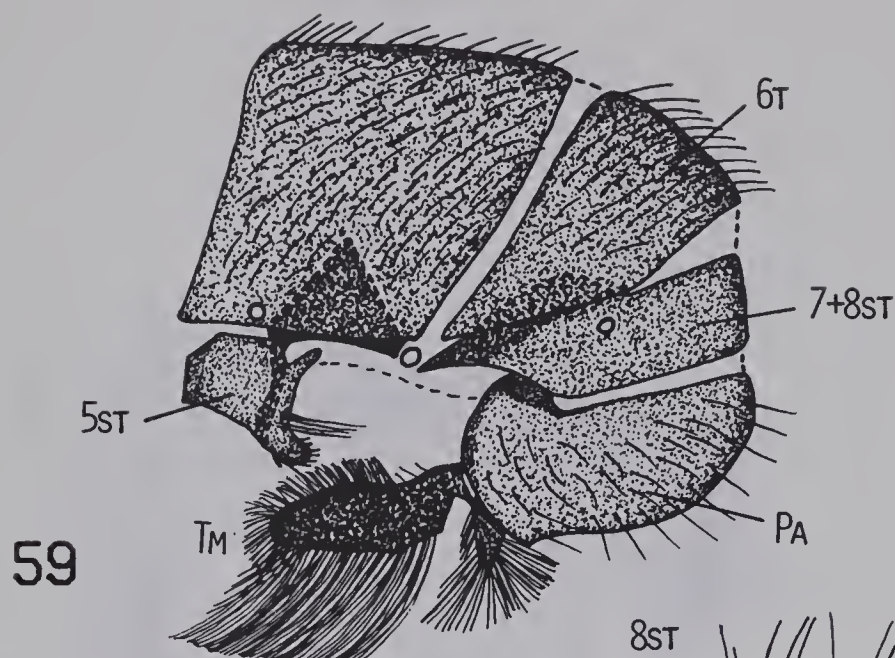
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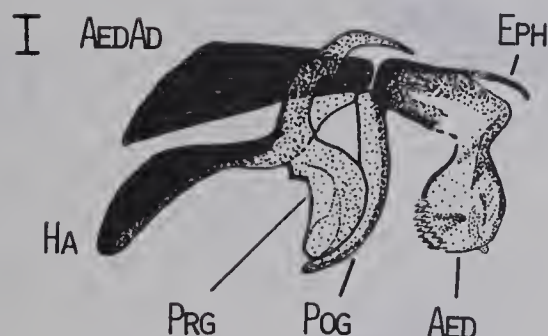
Figs. 54 - 58. 54. *Neotanypeza elegans* (Wiedemann) (Tanypezidae), aedeagus, hypandrium and associated structures (♂) in lateral view. 55. *Tanypeza luteipennis* Knab & Shannon (Tanypezidae), postabdomen (♂) in lateral view. 56. *Heteromyza atricornis* Meigen (Heteromyzidae), postabdomen (♂) in ventral view (with hypopygium removed). 57. *Heteromyza atricornis* Meigen, hypopygium (♂) in posterior view. 58. *Heteromyza atricornis* Meigen, aedeagus and associated structures (♂) in lateral view.

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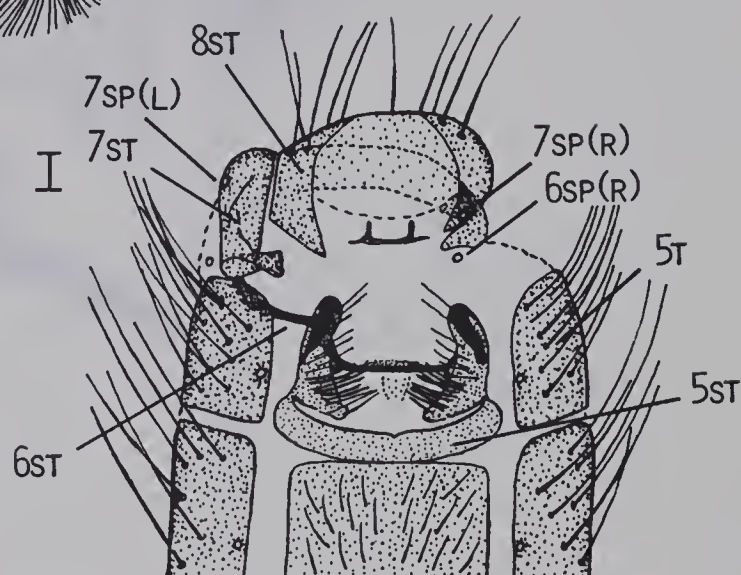
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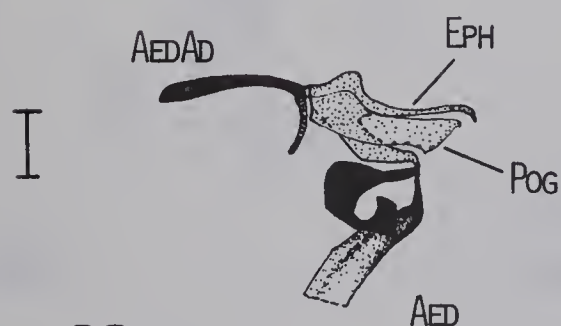
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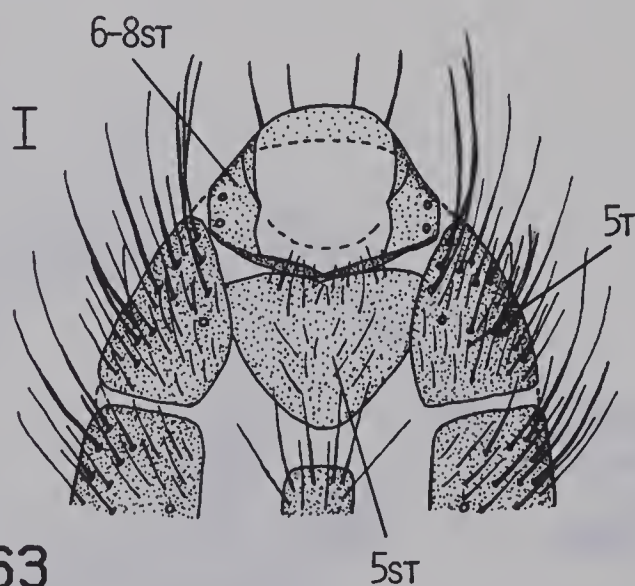
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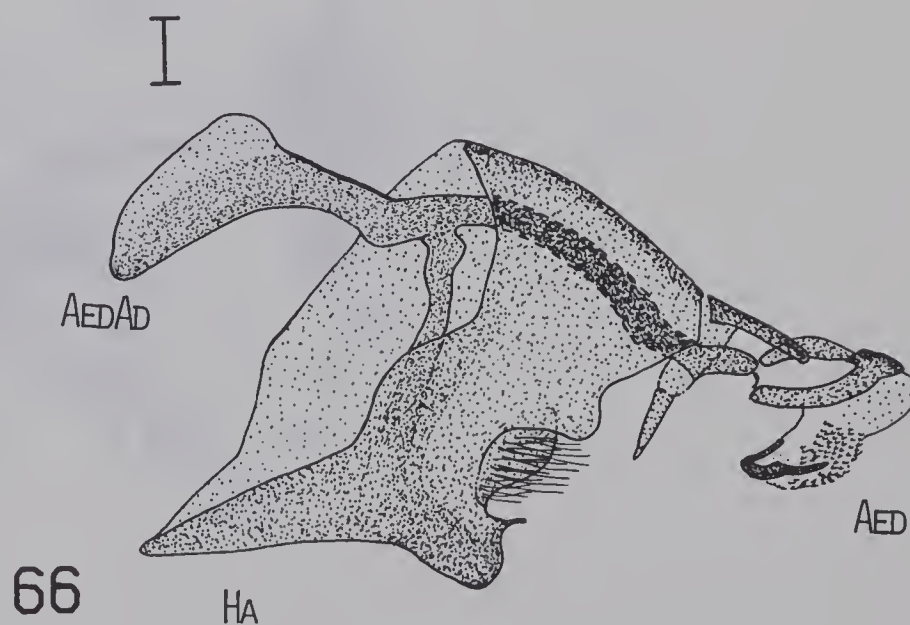
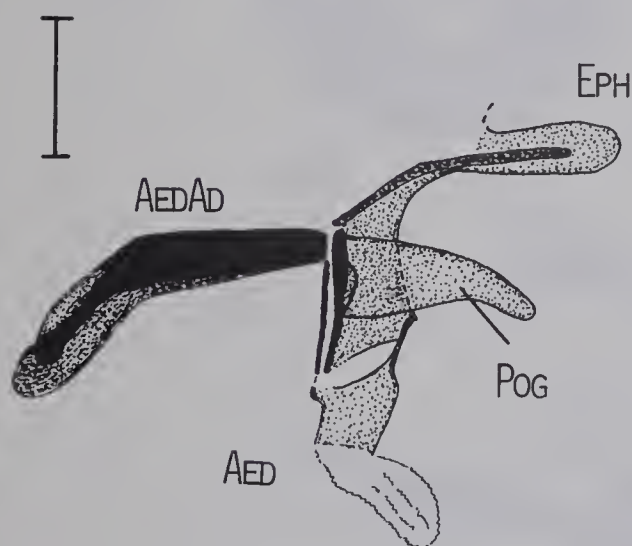
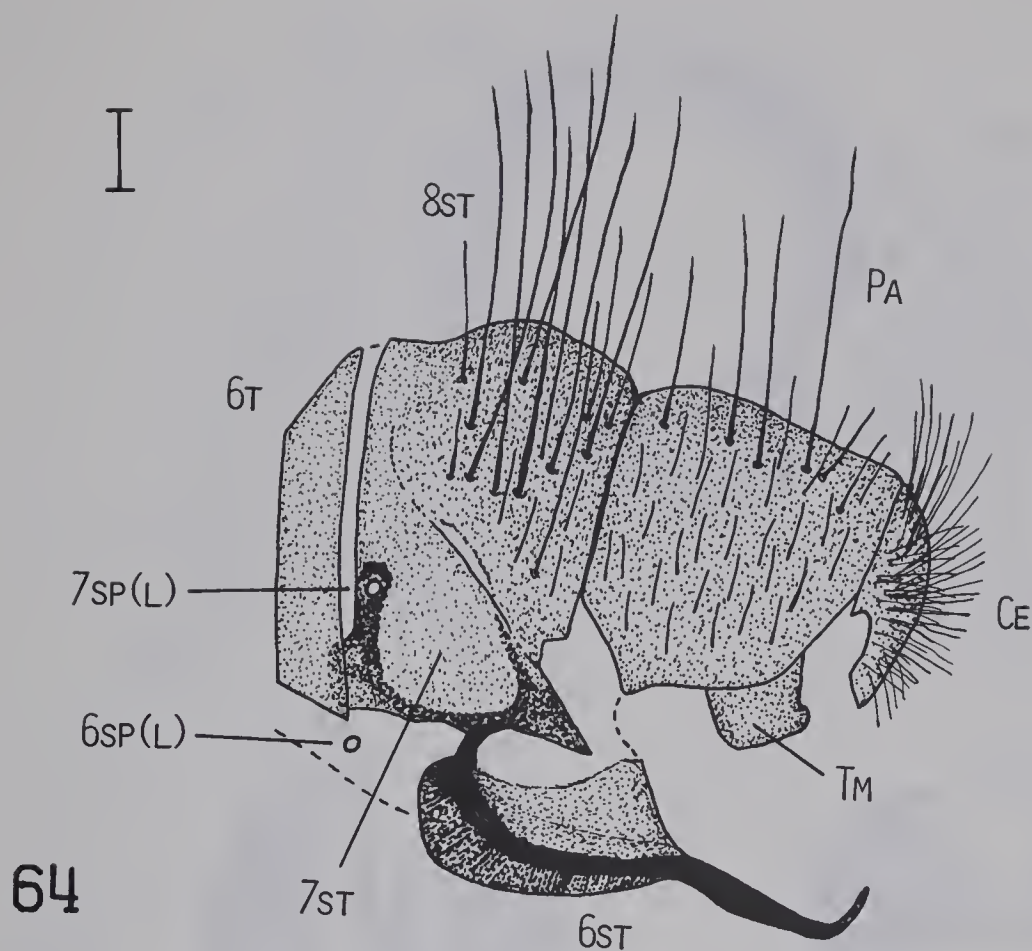
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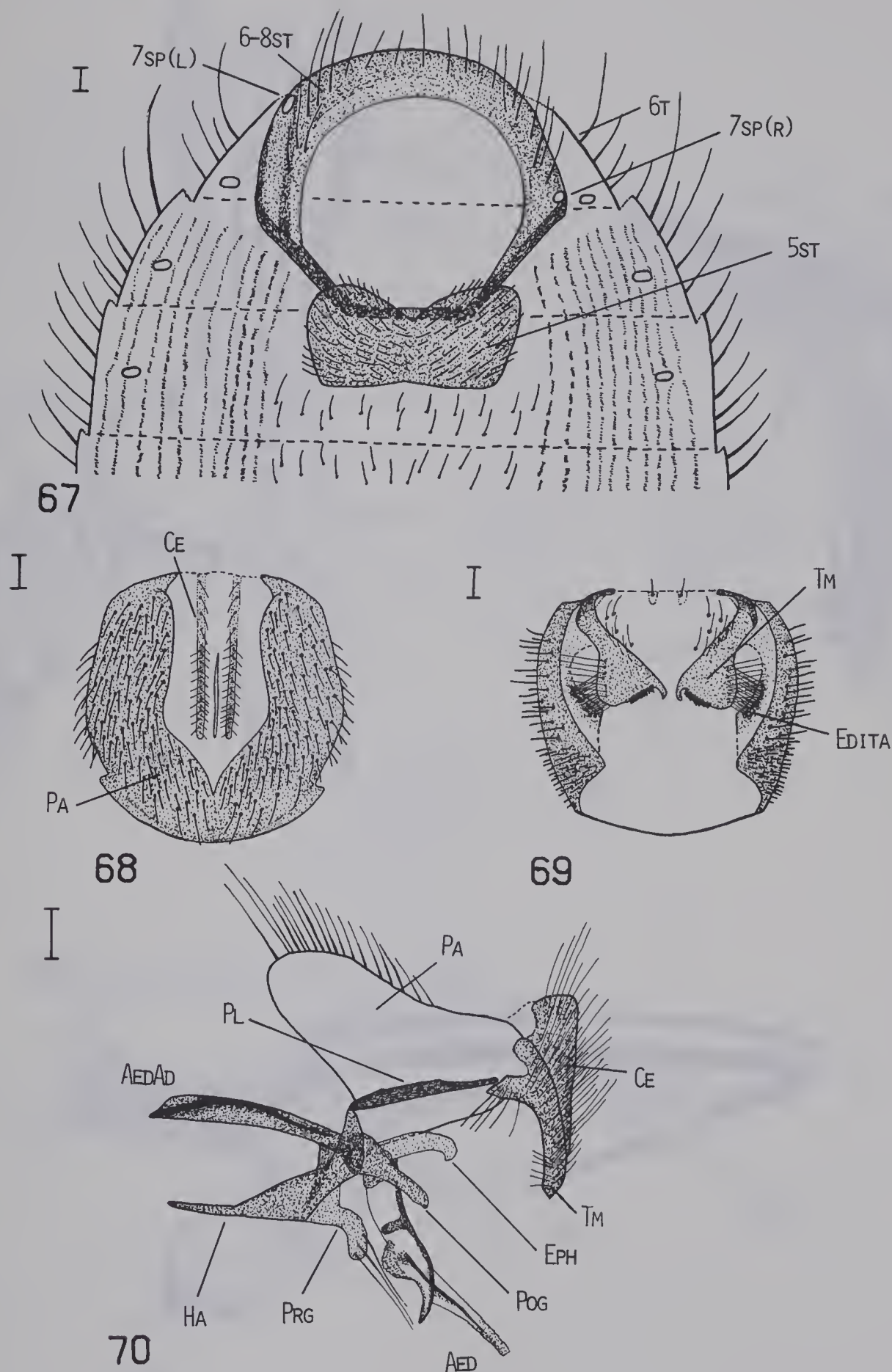
Figs. 59 - 63. 59. *Scatophaga aldrichi* (Malloch) (Scatophagidae), postabdomen (♂) in lateral view. 60. *Scatophaga aldrichi* (Malloch), aedeagus, hypandrium and associated structures (♂) in lateral view. 61. *Pegomya versicolor* (Meigen) (Anthomyiidae), postabdomen (♂) in ventral view (with hypopygium removed). 62. *Pegomya versicolor* (Meigen), aedeagus and associated structures (♂) in lateral view. 63. *Fannia canicularis* (L.) (Fanniidae), postabdomen (♂) in ventral view (with hypopygium removed).

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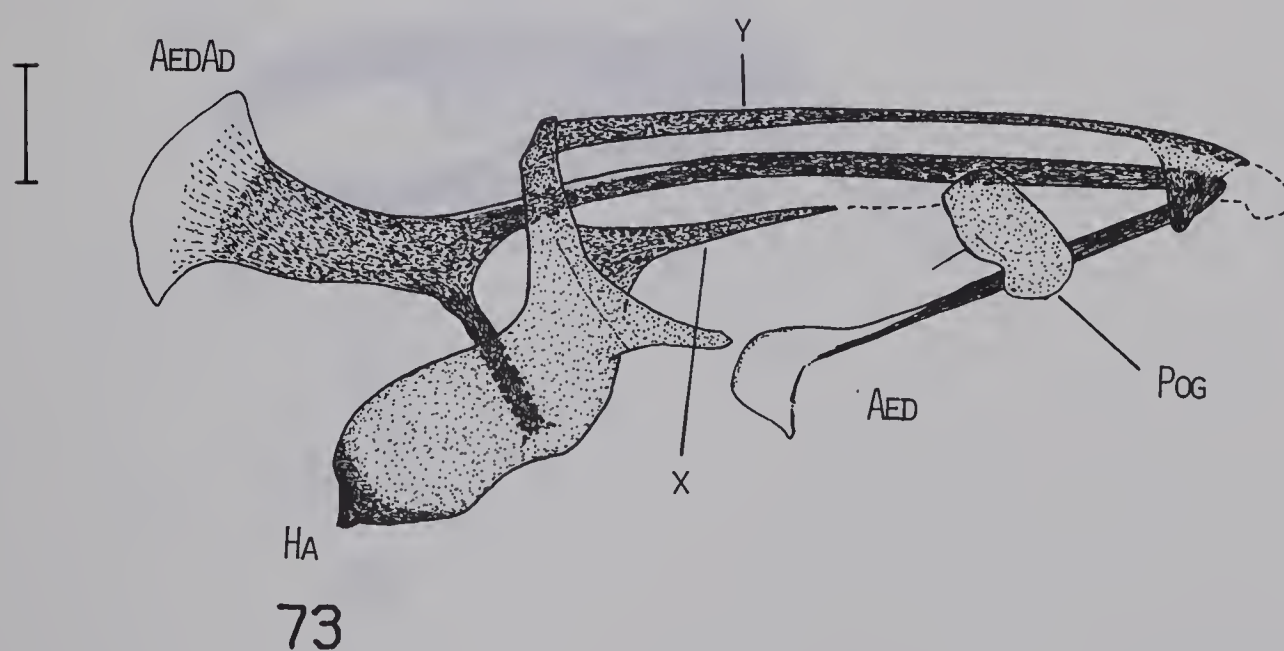
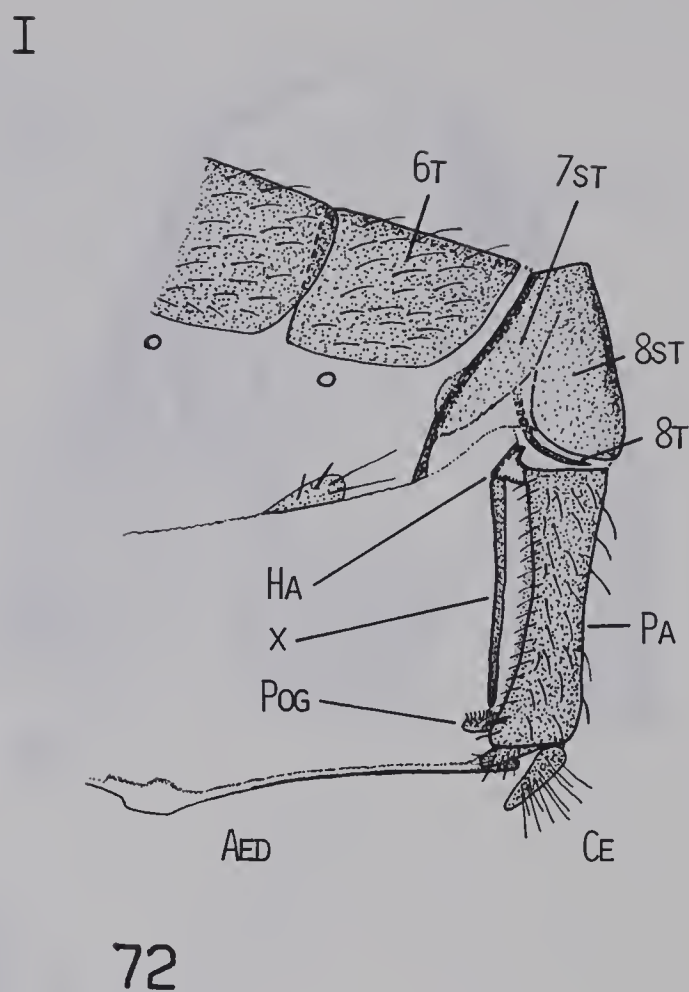
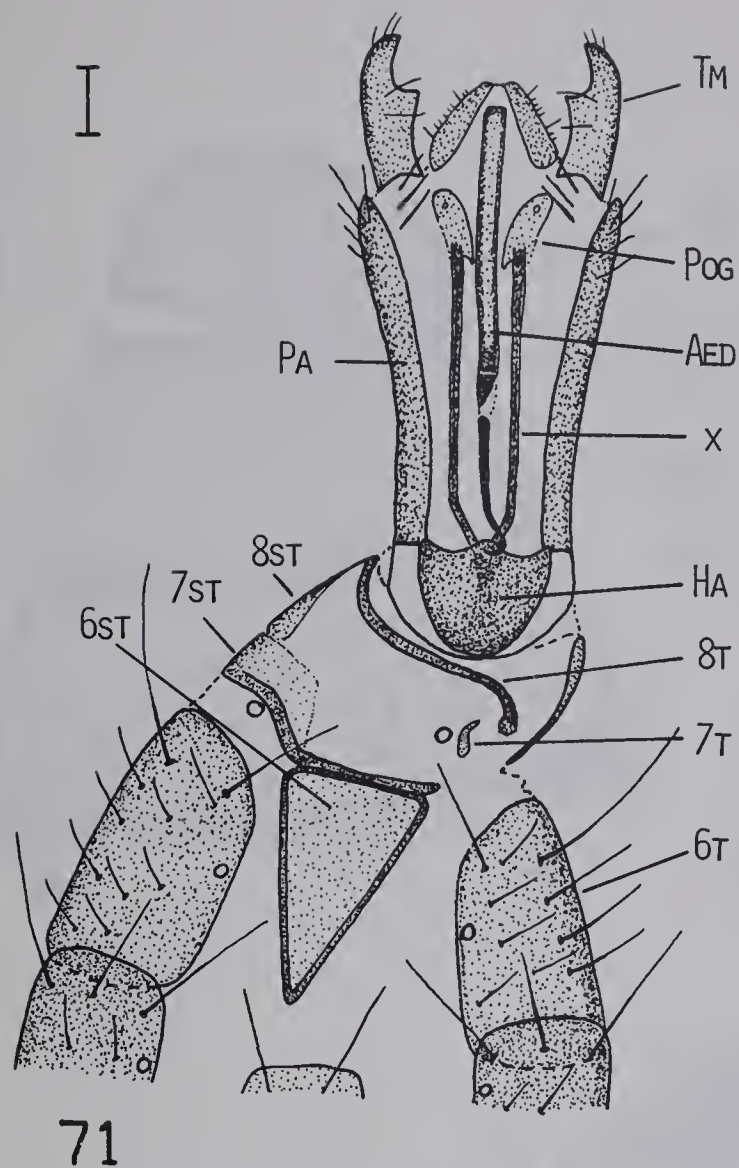


Figs. 64 - 66. 64. *Muscina assimilis* (Fallén) (Muscidae), postabdomen (♂) in lateral view. 65. *Muscina assimilis* (Fallén), aedeagus and associated structures (♂) in lateral view. 66. *Glossina morsitans* Westwood (Glossinidae), aedeagus, hypandrium and associated structures (♂) in lateral view.

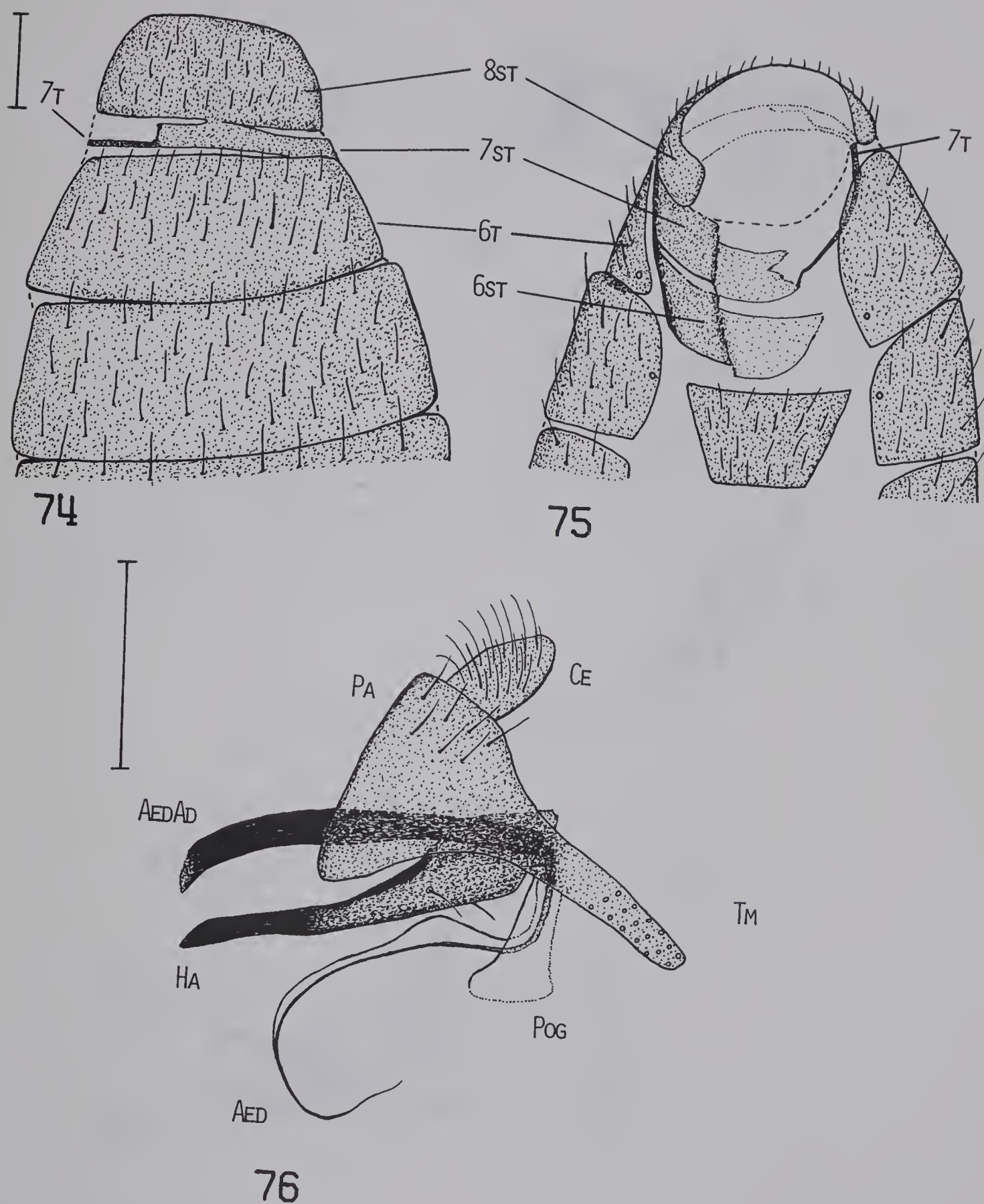
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Figs. 67 - 70. 67. *Glossina morsitans* Westwood, abdomen (part) (♂) in ventral view (with hypopygium removed). 68. *Glossina morsitans* Westwood, hypopygium (♂) in dorsal view. 69. *Glossina morsitans* Westwood, perianthrium, telomeres and associated structures (♂) in ventral view. 70. *Eucalliphora lilaea* (Walker) (Tachinidae s.l.), hypopygium (♂) in lateral view (with left side of perianthrium removed). (Scale lines 0.1 mm.)

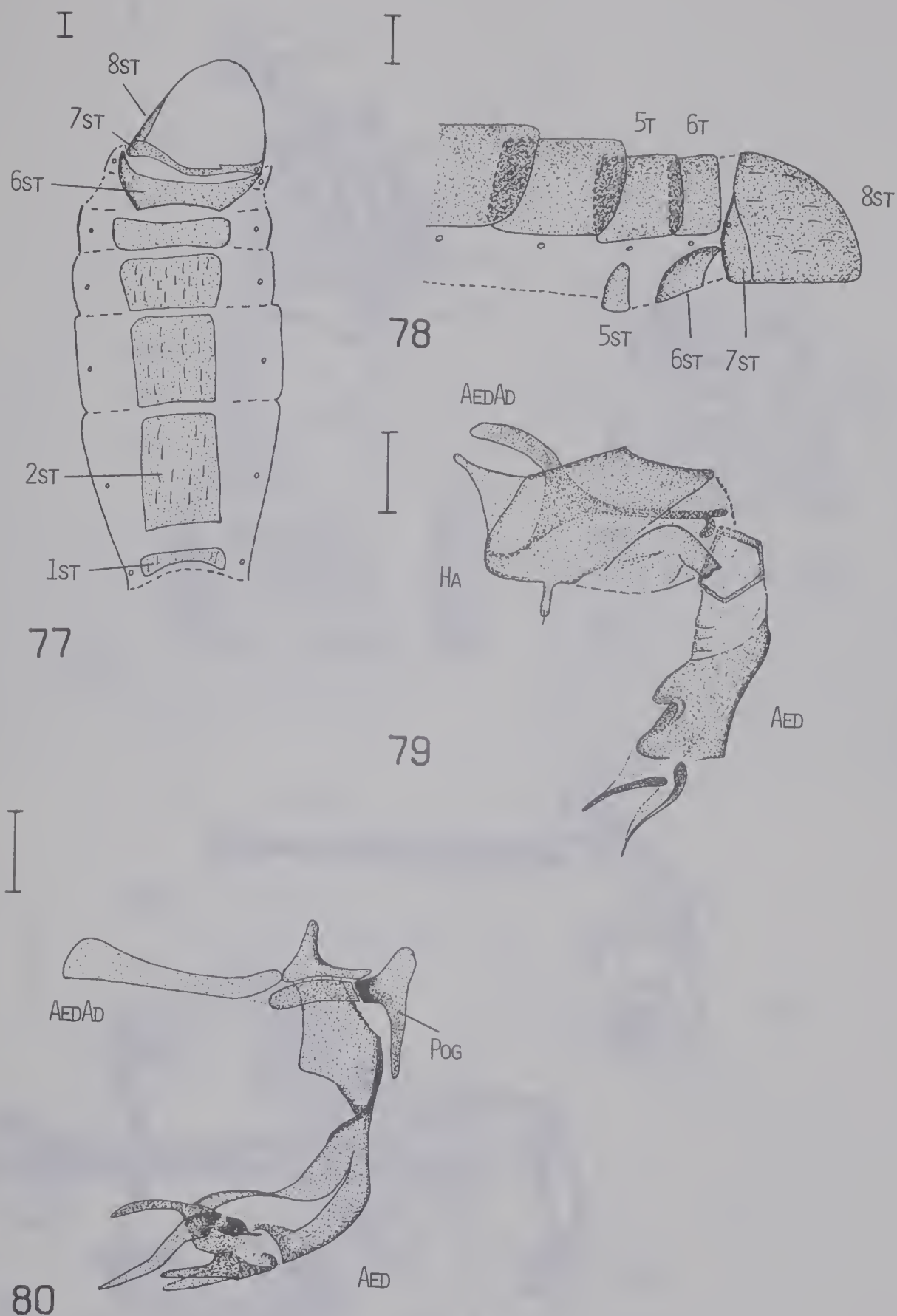


Figs. 71 - 73. 71. *Heloclusia imperfecta* Malloch (Cypselosomatidae), postabdomen (♂) in ventral view (with hypopygium turned back). 72. *Gymnonerius fuscus ceylanicus* Hennig (Neriidae), postabdomen (♂) in lateral view. 73. *Micropeza lineata* Van Duzee (Micropezidae), aedeagus, hypandrium and associated structures (♂) in lateral view. (Scale lines 0.1 mm.)



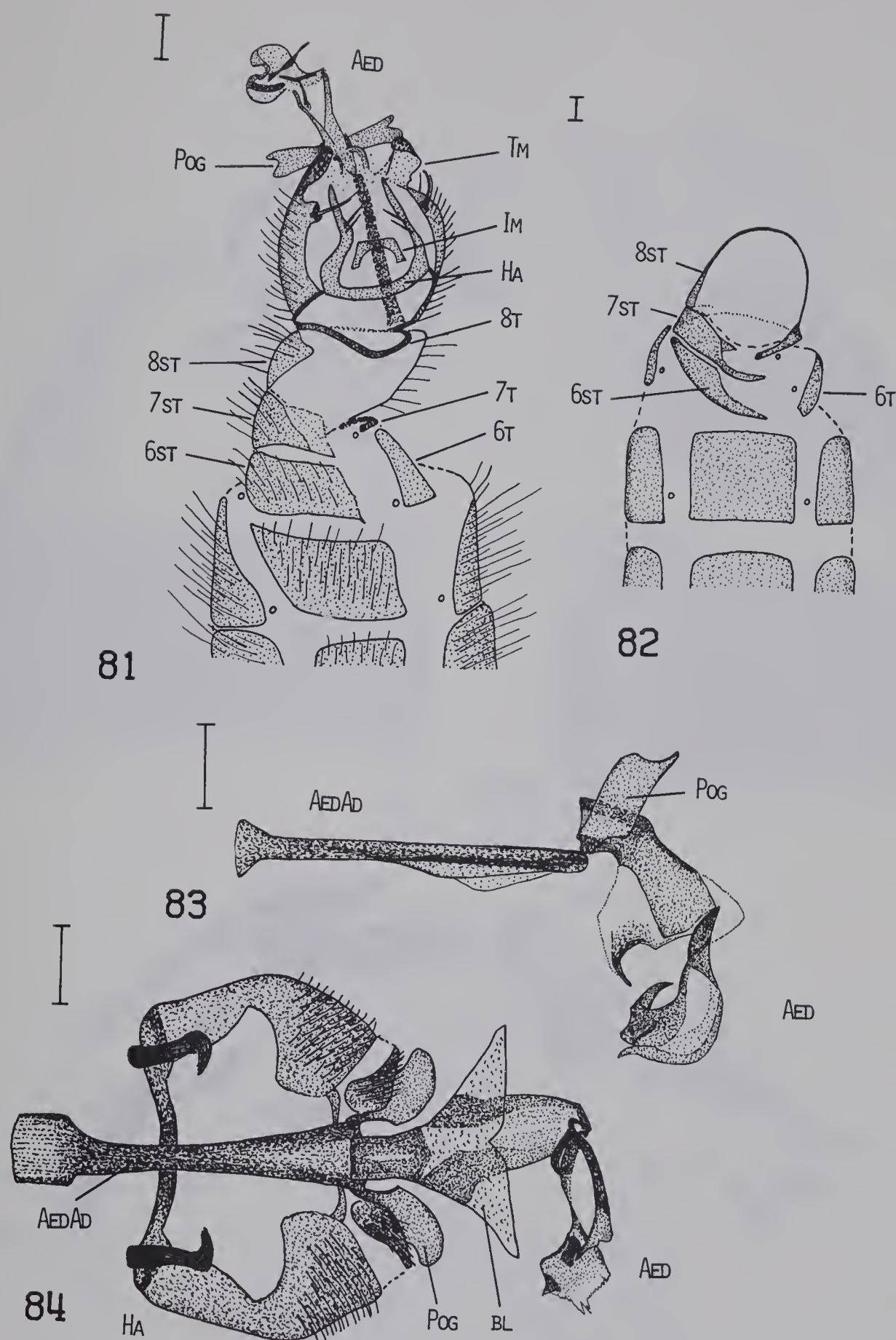
Figs. 74 - 76. 74. *Australimyza anisotomae* Harrison (Australimyzidae), postabdomen (♂) in dorsal view (with hypopygium removed). 75. *Australimyza anisotomae* Harrison, postabdomen (♂) in ventral view (with hypopygium removed). 76. *Australimyza anisotomae* Harrison, hypopygium (♂) in lateral view.

(Scale lines 0.1 mm.)



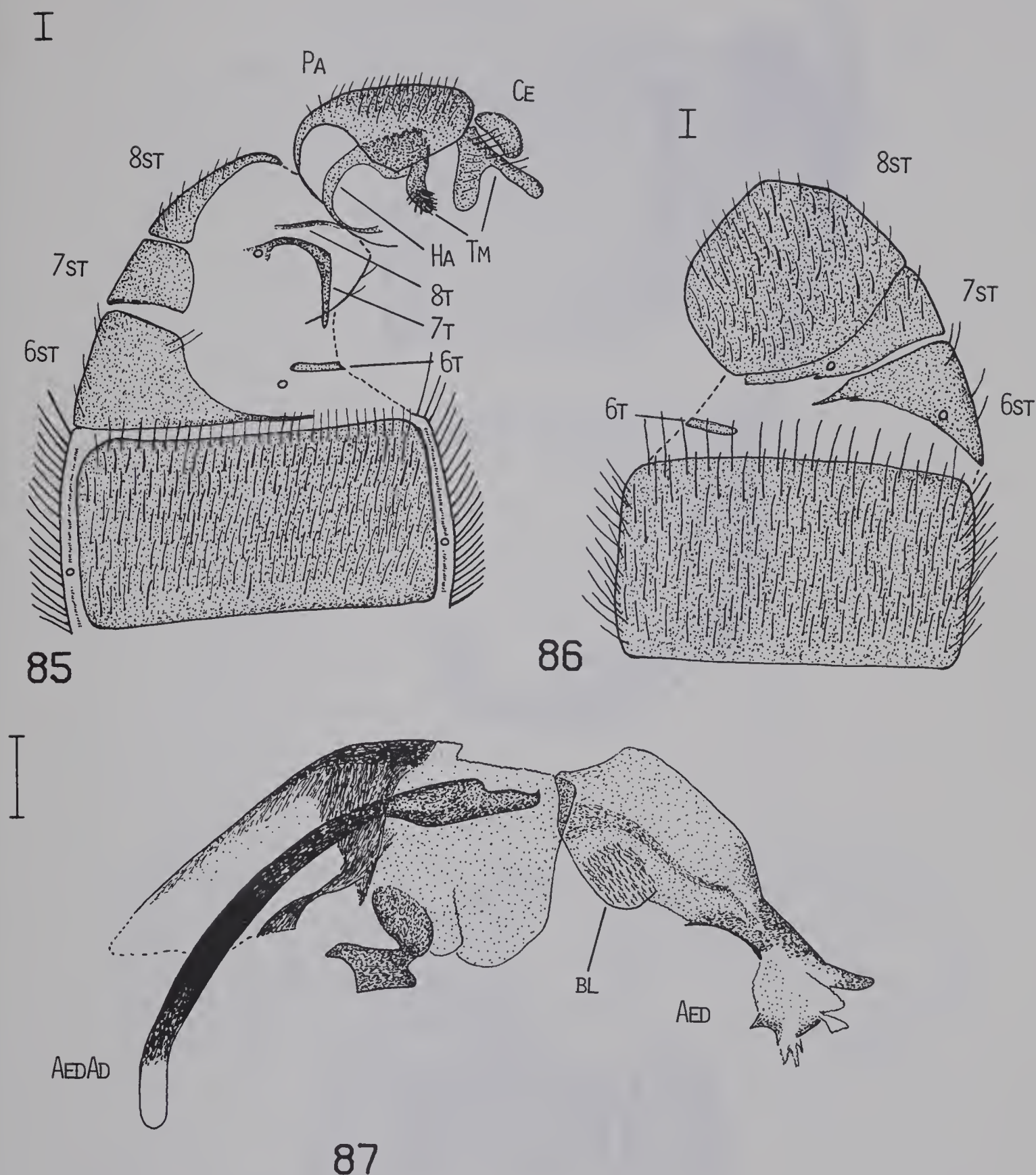
Figs. 77 - 80. 77. *Centrioncus prodiopsis* Speiser (Diopsidae), abdomen (♂) in ventral view (with hypopygium removed). 78. *Centrioncus prodiopsis* Speiser, abdomen (part) (♂) in lateral view (with hypopygium removed). 79. *Centrioncus prodiopsis* Speiser, aedeagus, hypandrium and associated structures (♂) in lateral view. 80. *Syringogaster rufa* Cresson (Syringogastridae), aedeagus and associated structures (♂) in lateral view.

(Scale lines 0.1 mm.)



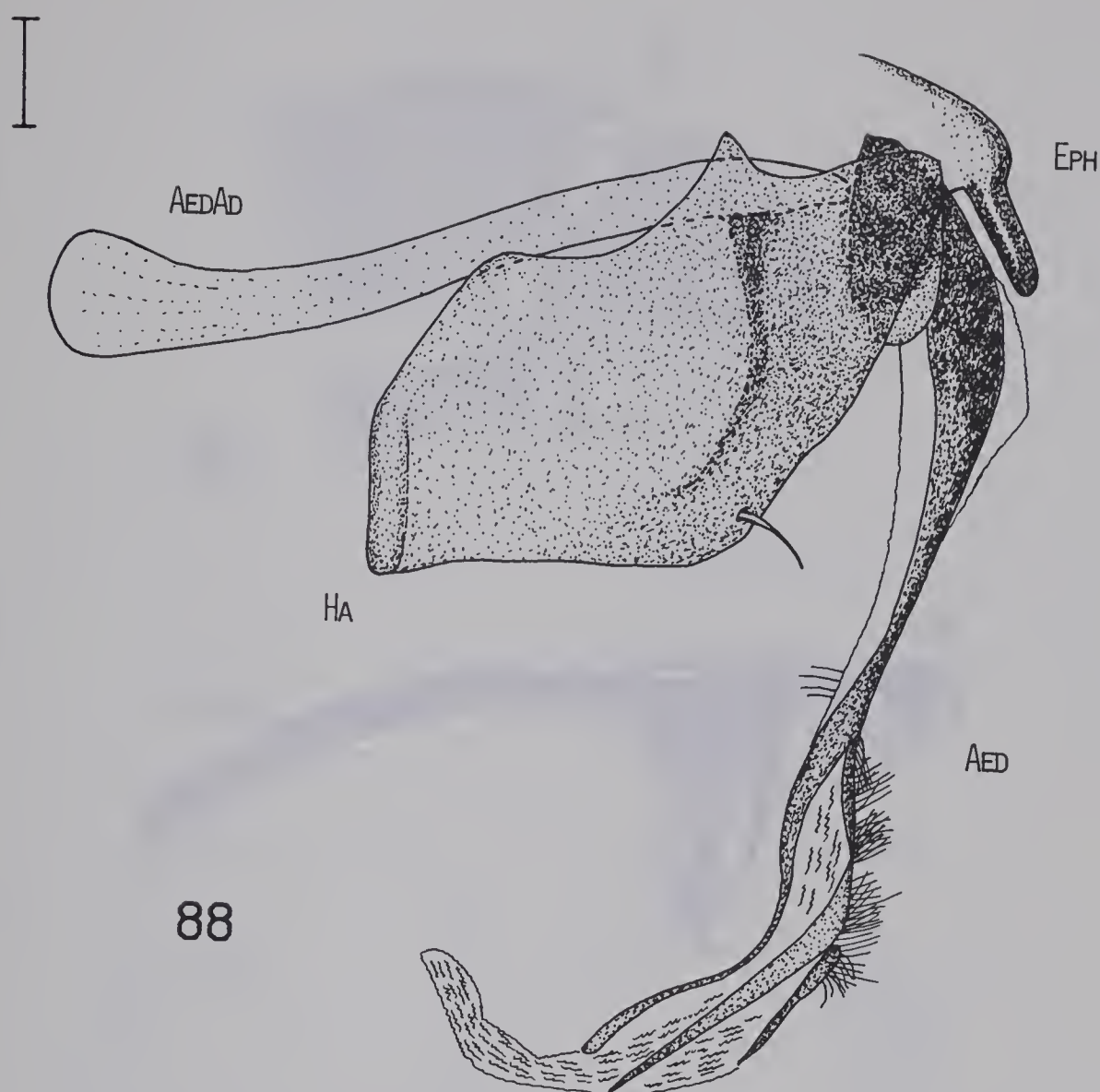
Figs. 81 - 84. 81. *Malacomyia sciomyzina* (Haliday) (Coelopidae), postabdomen (♂) in ventral view (with hypopygium turned back). 82. *Heterocheila hannai* (Cole) (Coelopidae), postabdomen (♂) in ventral view (with hypopygium removed, and with the dense pubescence omitted). 83. *Malacomyia sciomyzina* (Haliday), aedeagus and associated structures (♂) in lateral view. 84. *Heterocheila hannai* (Cole), aedeagus, hypandrium and associated structures (♂) in dorsal view (with aedeagus in copulatory position).

(Scale lines 0.1 mm.)

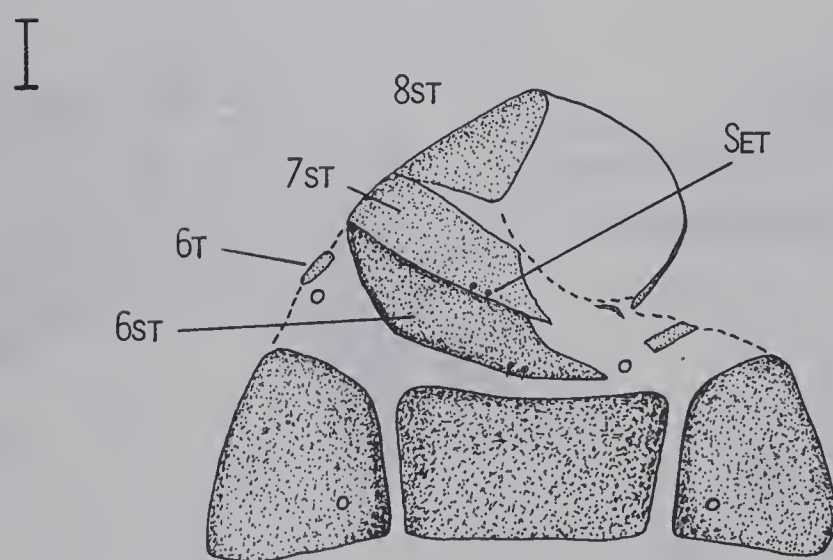


Figs. 85 - 87. 85. *Pelidnoptera nigripennis* (F.) (Phaeomyiidae), postabdomen (♂) in ventral view, with the left side of the hypopygium (turned laterally). 86. *Pelidnoptera nigripennis* (F.), postabdomen (♂) in dorsal view (with hypopygium removed). 87. *Pelidnoptera nigripennis* (F.), aedeagus and associated structures (♂) in lateral view.

(Scale lines 0.1 mm.)

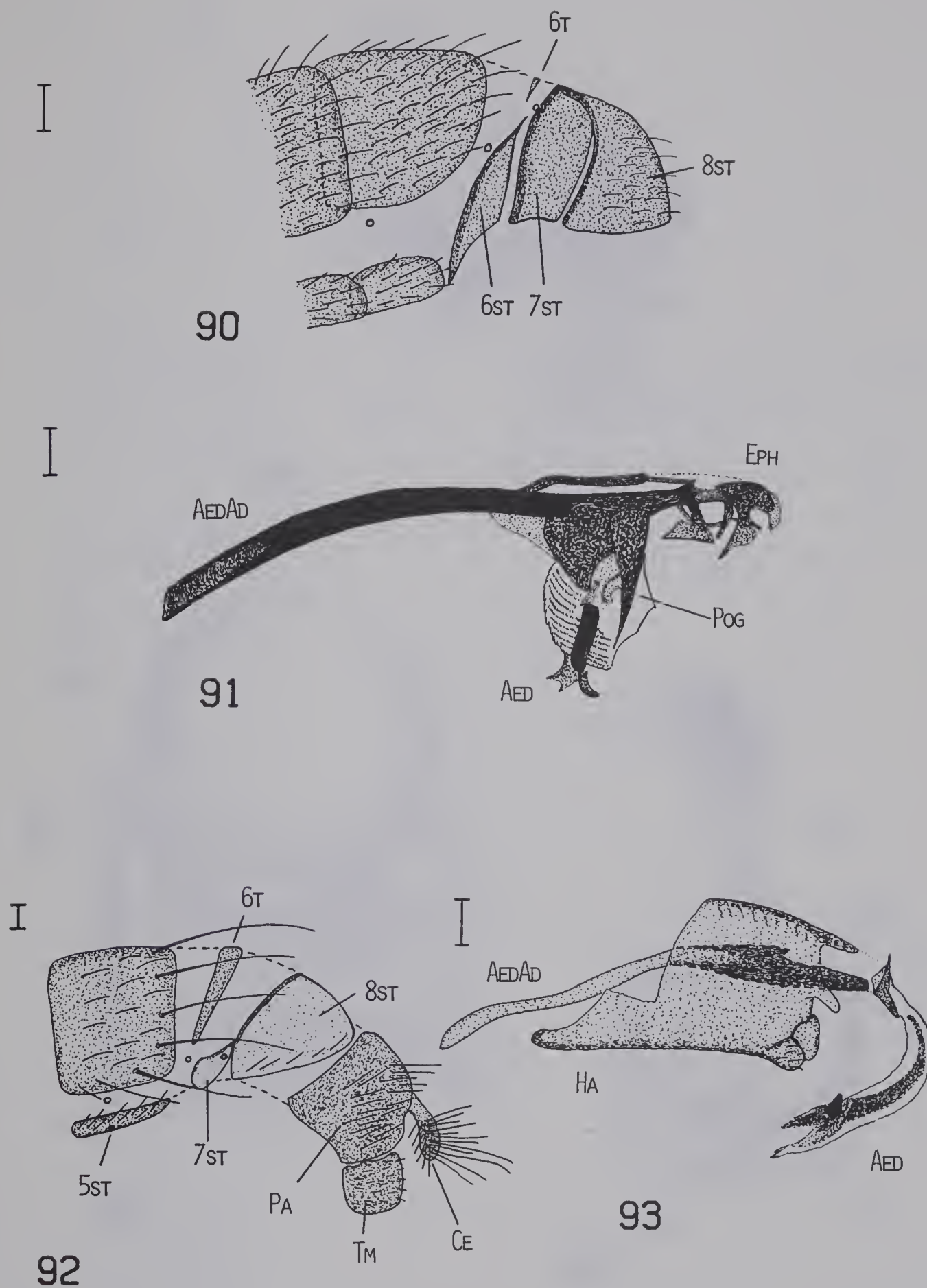


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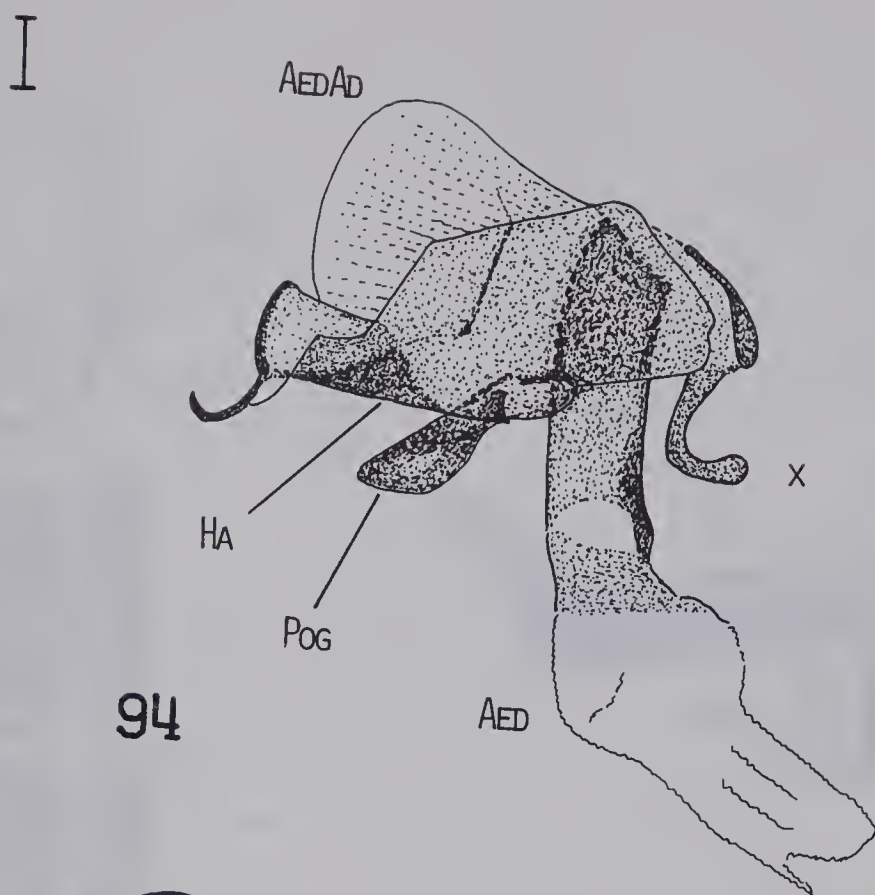
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Figs. 88 - 89. 88. *Maorimyia bipunctata* (Hutton) (Dryomyzidae), aedeagus, hypandrium and associated structures (♂) in lateral view. 89. *Dryomyza anilis* (Fallén) (Dryomyzidae), postabdomen (♂) in ventral view (with hypopygium removed, and with the dense pubescence omitted). (Scale lines 0.1 mm.)

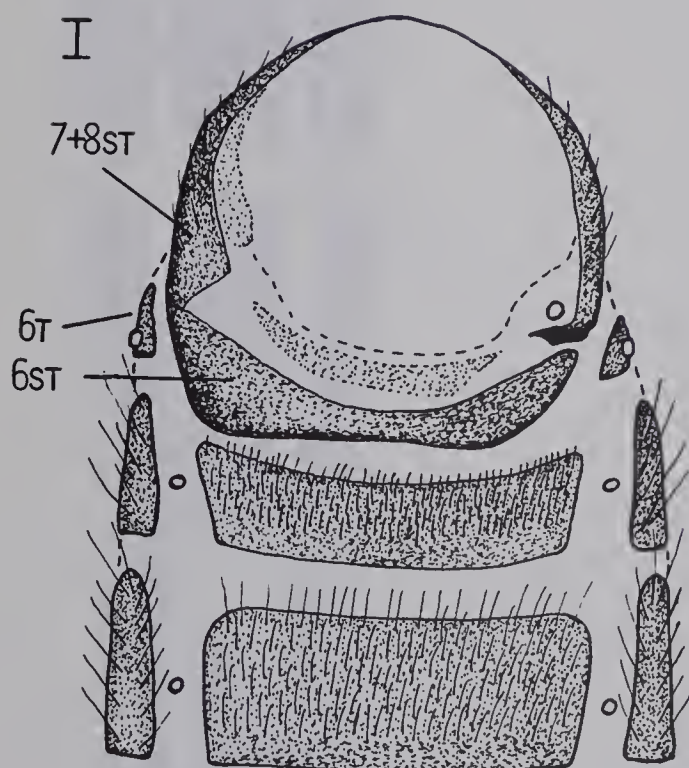


Figs. 90 - 93. 90. *Pteromicra apicata* (Loew) (Sciomyzidae), postabdomen (♂) in lateral view (with hypopygium removed). 91. *Pherbellia albocostata* (Fallén) (Sciomyzidae), aedeagus and associated structures (♂) in lateral view. 92. *Helosciomyza subspiniosta* Tonnoir & Malloch (Helosciomyzidae), postabdomen (♂) in lateral view. 93. *Helosciomyza subspiniosta* Tonnoir & Malloch, aedeagus, hypandrium and associated structures (♂) in lateral view.

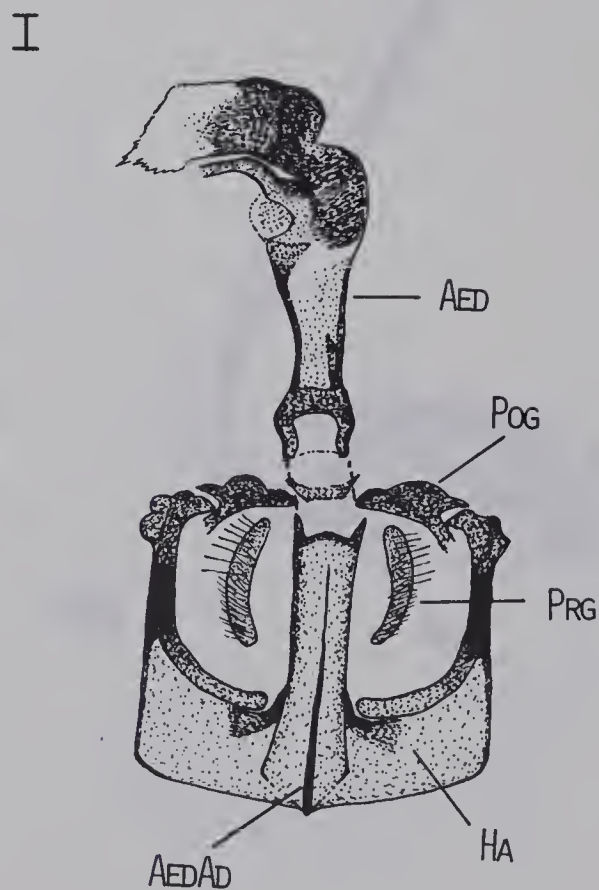
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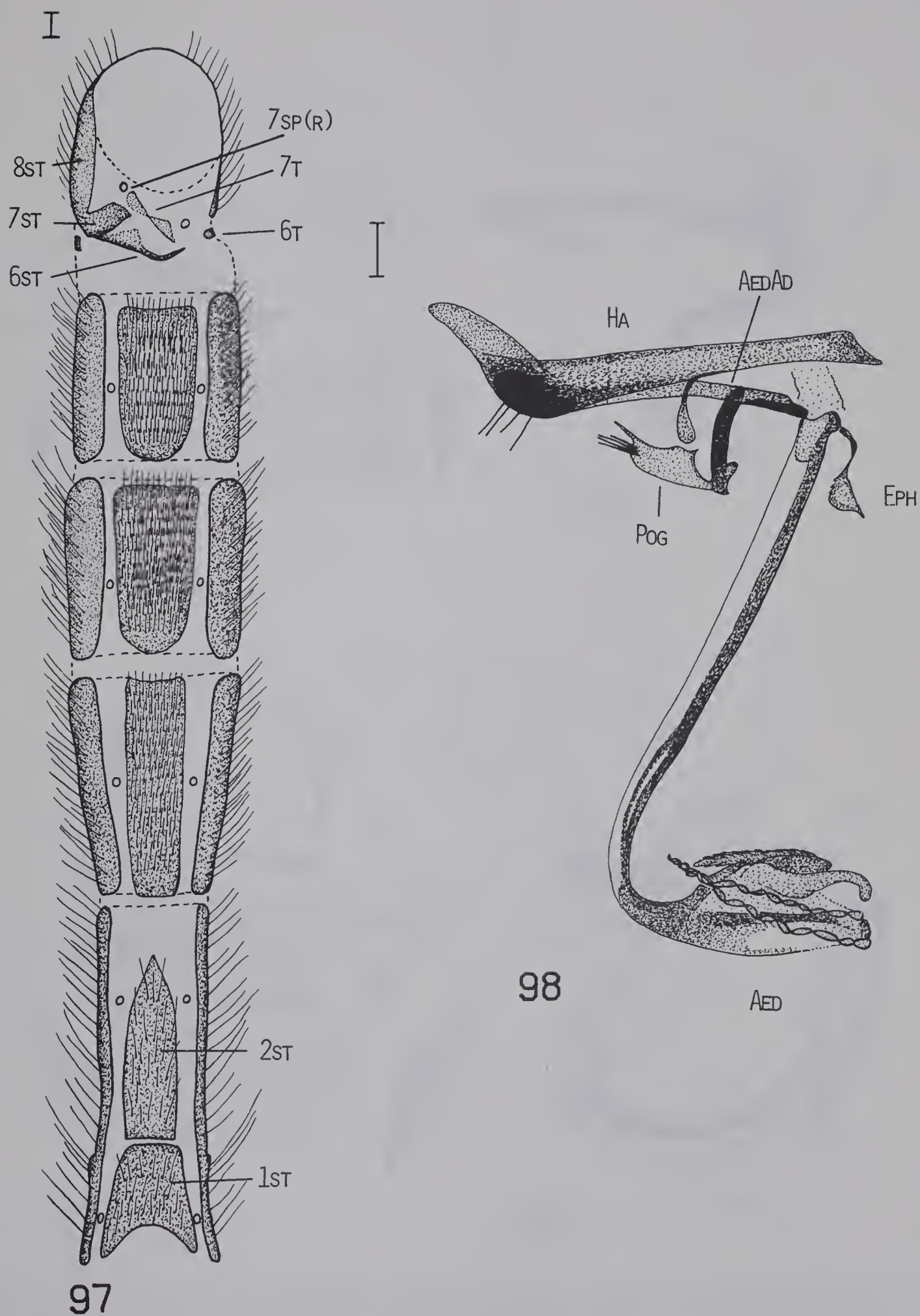
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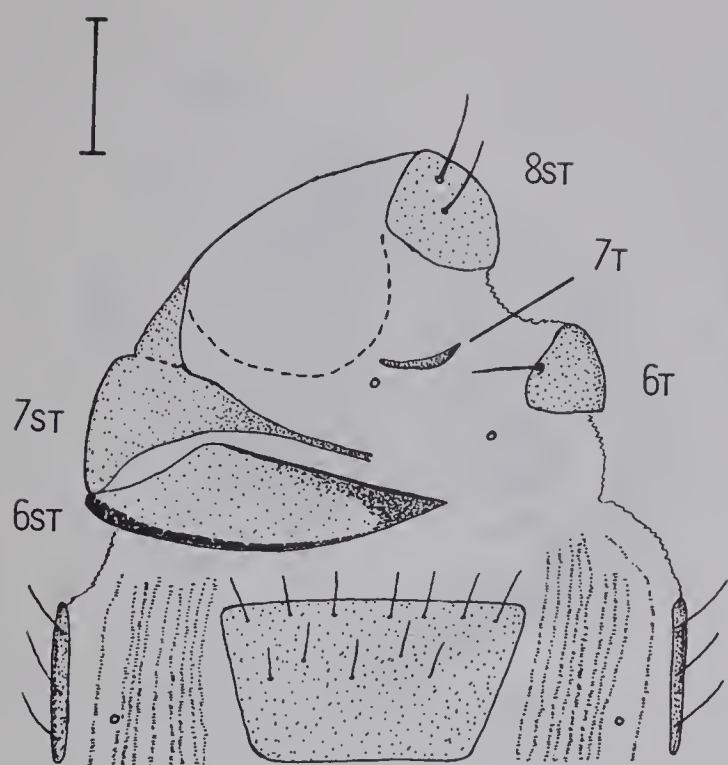
Figs. 94 - 96. 94. *Rhytidops floridensis* (Aldrich) (Ropalomeridae), aedeagus, hypandrium and associated structures (♂) in lateral view. 95. *Orygma luctuosum* Meigen (Sepsidae), postabdomen (♂) in ventral view (with hypopygium removed). 96. *Orygma luctuosum* Meigen, aedeagus, hypandrium and associated structures (♂) in ventral view (with aedeagus in copulatory position).

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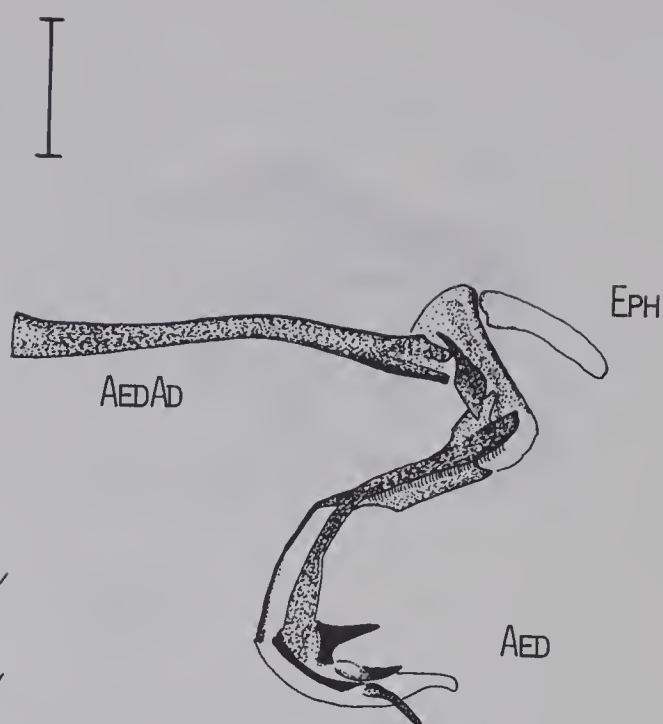


Figs. 97 - 98. 97. *Megamerina dolium* (F.) (Megamerinidae), abdomen (♂) in ventral view (with hypopygium removed). 98. *Megamerina dolium* (F.), aedeagus, hypandrium and associated structures (♂) in lateral view.

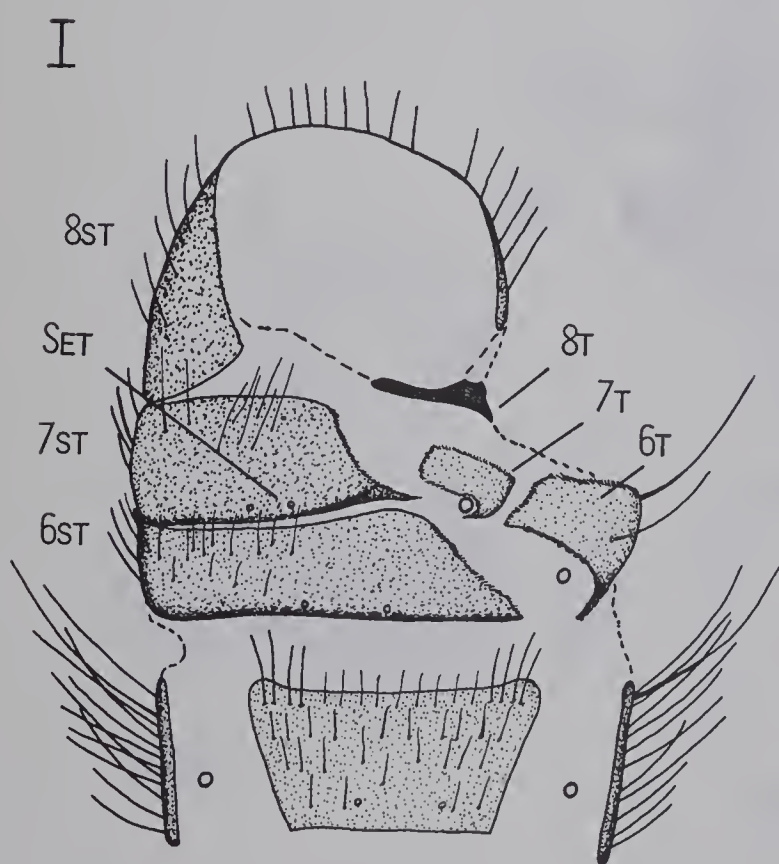
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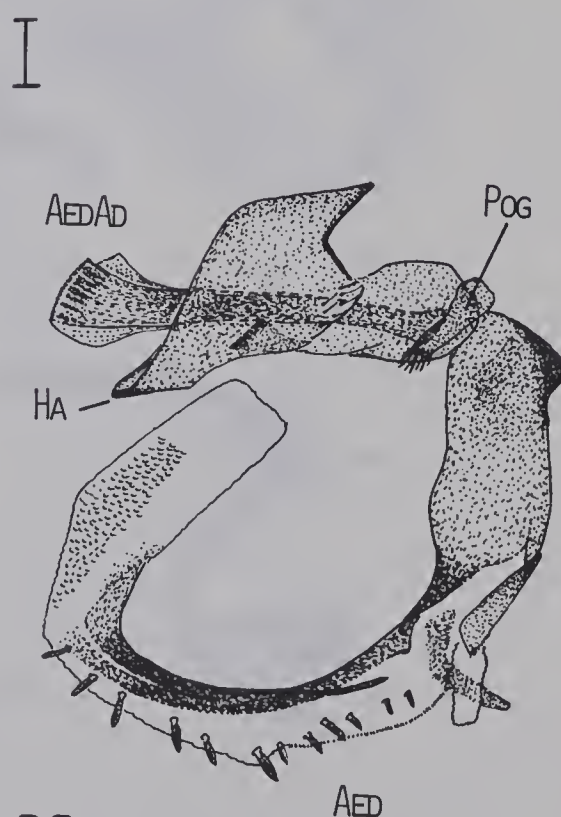
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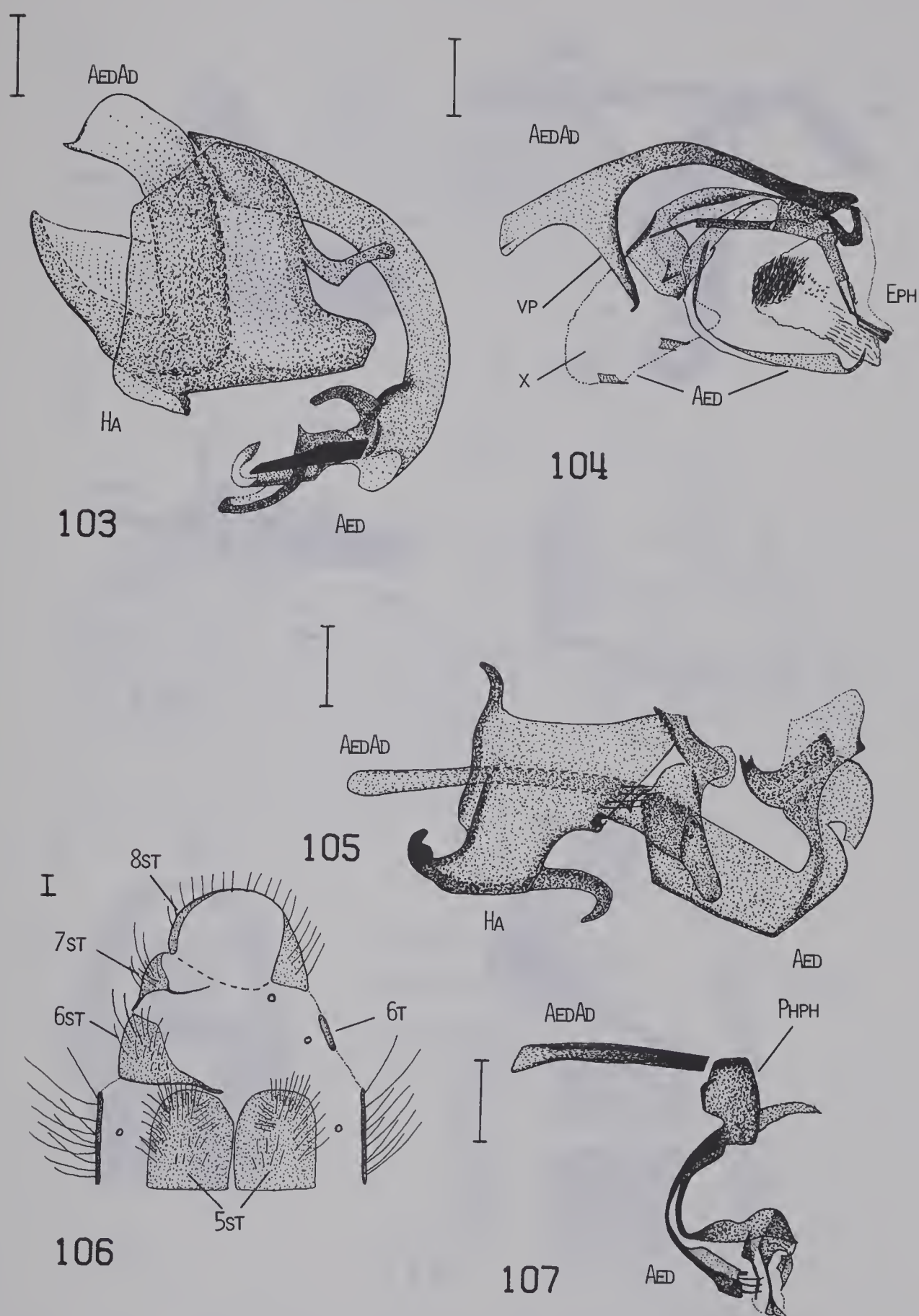
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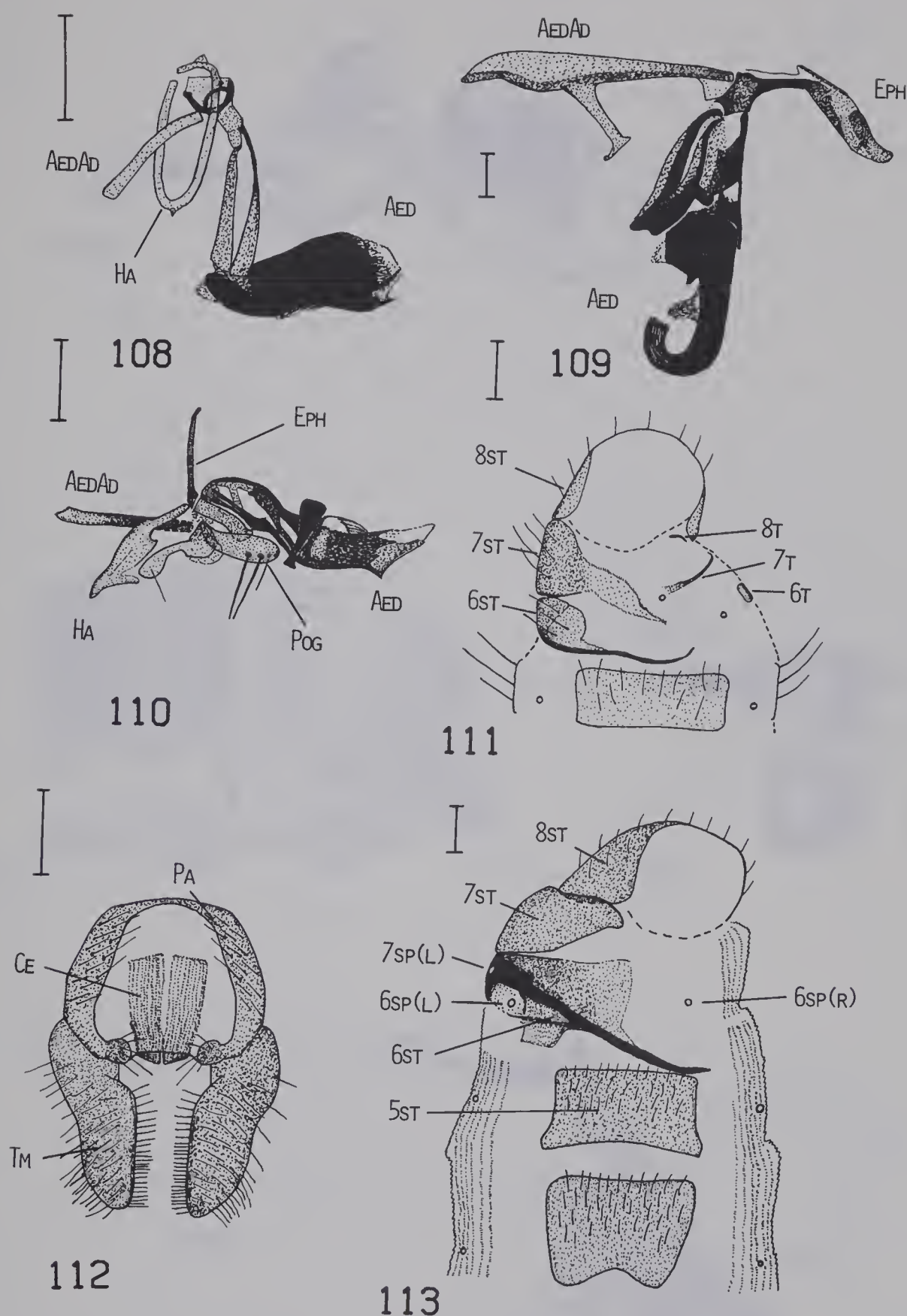
Figs. 99 - 102. 99. *Cremifania nigrocellulata* Czerny (Cremifaniidae), postabdomen (♂) in ventral view (with hypopygium removed). 100. *Cremifania nigrocellulata* Czerny, aedeagus and associated structures (♂) in lateral view. 101. *Orbellia tokyoensis* Czerny (Heleomyzidae), postabdomen (♂) in ventral view (with hypopygium removed). 102. *Orbellia tokyoensis* Czerny, aedeagus, hypandrium and associated structures (♂) in lateral view.

(Scale lines 0.1 mm.)



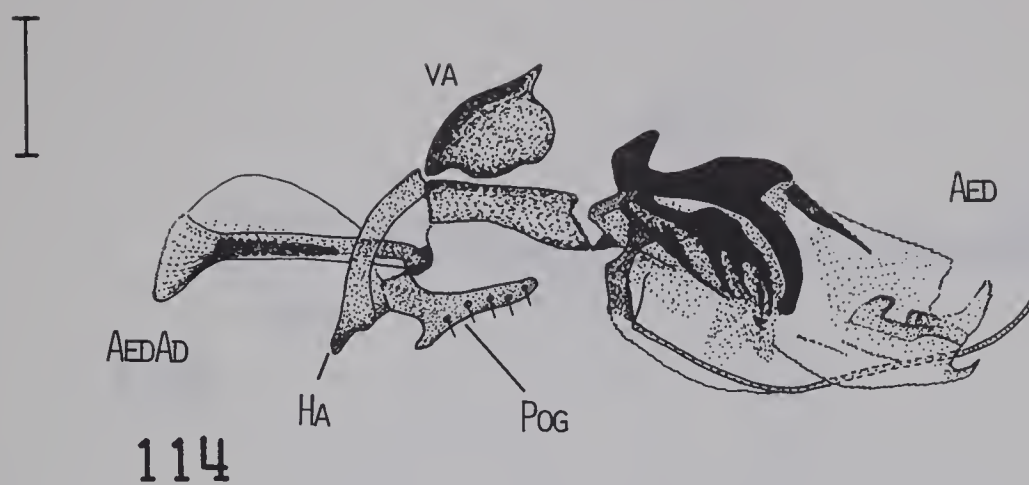
Figs. 103 - 107. 103. *Allophylopsis scutellata* (Hutton) (Heleomyzidae), aedeagus, hypandrium and associated structures (♂) in lateral view. 104. *Anthomyza* sp. (Anthomyzidae), aedeagus and associated structures (♂) in lateral view. 105. *Tapeigaster marginifrons* Bezzi (Rhinotoridae), aedeagus, hypandrium and associated structures (♂) in lateral view. 106. *Tapeigaster marginifrons* Bezzi, postabdomen (♂) in ventral view (with hypopygium removed). 107. *Trixoscelis* sp. (Trixoscelididae), aedeagus and associated structures (♂) in lateral view.

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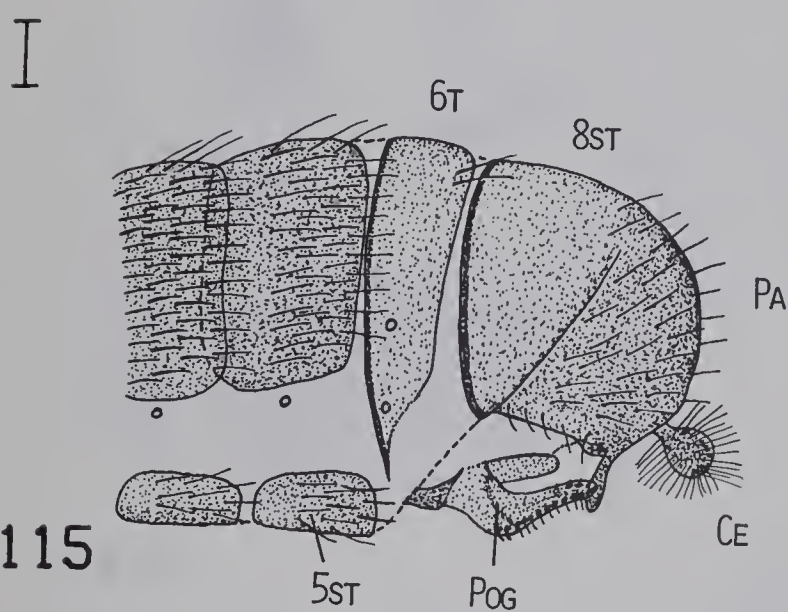


Figs. 108 - 113. 108. *Asteia amoena* Meigen (Asteiidae), aedeagus, hypandrium and associated structures (♂) in anterolateral view. 109. *Opomyza germinationis* (L.) (Opomyzidae), aedeagus and associated structures (♂) in lateral view. 110. *Borboropsis puberula* (Zetterstedt) (Borboropsidae), aedeagus, hypandrium and associated structures (♂) in lateral view (with aedeagus in copulatory position). 111. *Borboropsis puberula* (Zetterstedt), postabdomen (♂) in ventral view (with hypopygium removed). 112. *Sphaerocera curvipes* Latreille (Sphaeroceridae), hypopygium (♂) in posterior view. 113. *Sphaerocera curvipes* Latreille, abdomen (part) (♂) in ventral view (with hypopygium removed).

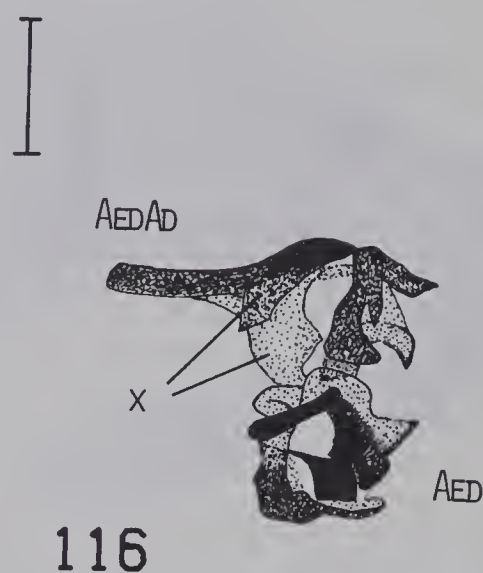
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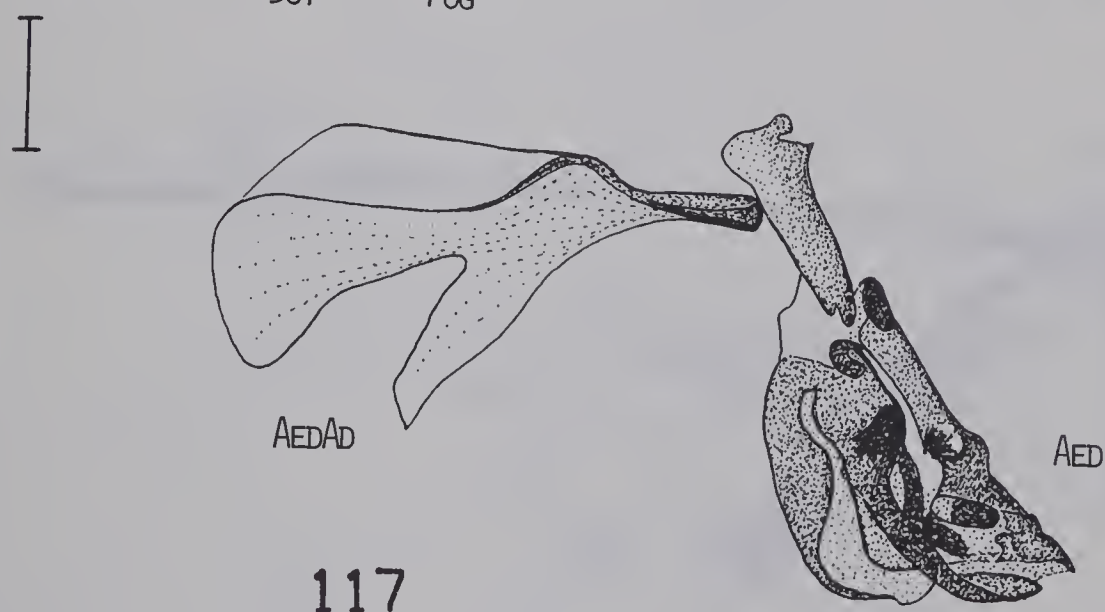
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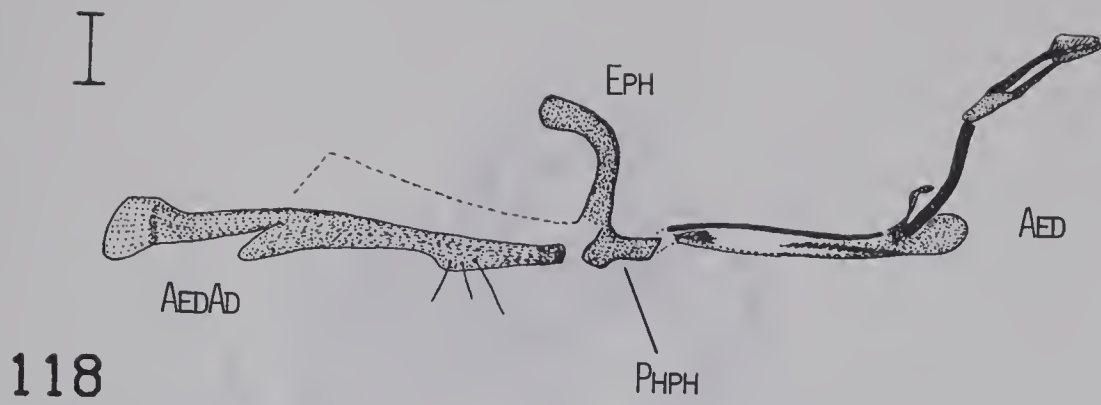
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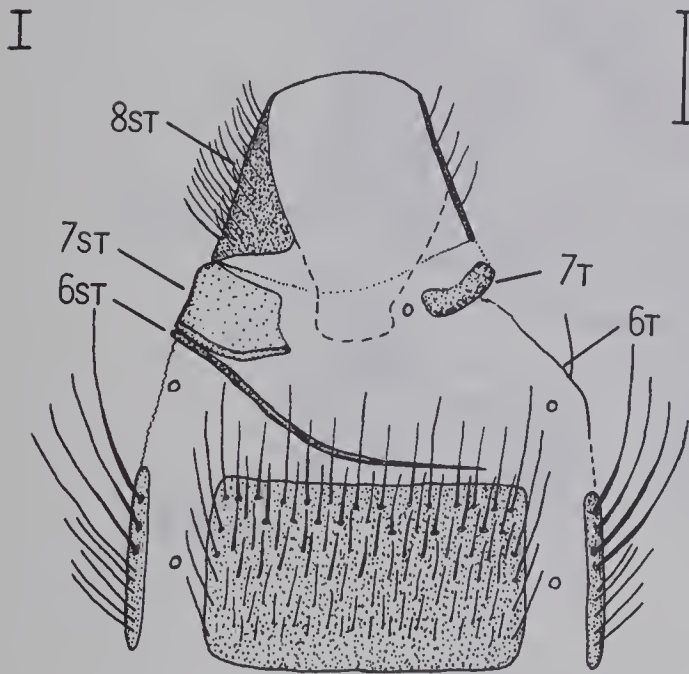
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Figs. 114 - 117. 114. *Sphaerocera curvipes* Latreille, aedeagus, hypandrium and associated structures (♂) in lateral view (with aedeagus in copulatory position). 115. *Chyromya flava* (L.) (Chyromyidae), postabdomen (♂) in lateral view. 116. *Cyamops nebulosus* Melander (Aulacigastriidae), aedeagus and associated structures (♂) in lateral view. 117. *Chyromya flava* (L.) (Chyromyidae), aedeagus and associated structures (♂) in lateral view.

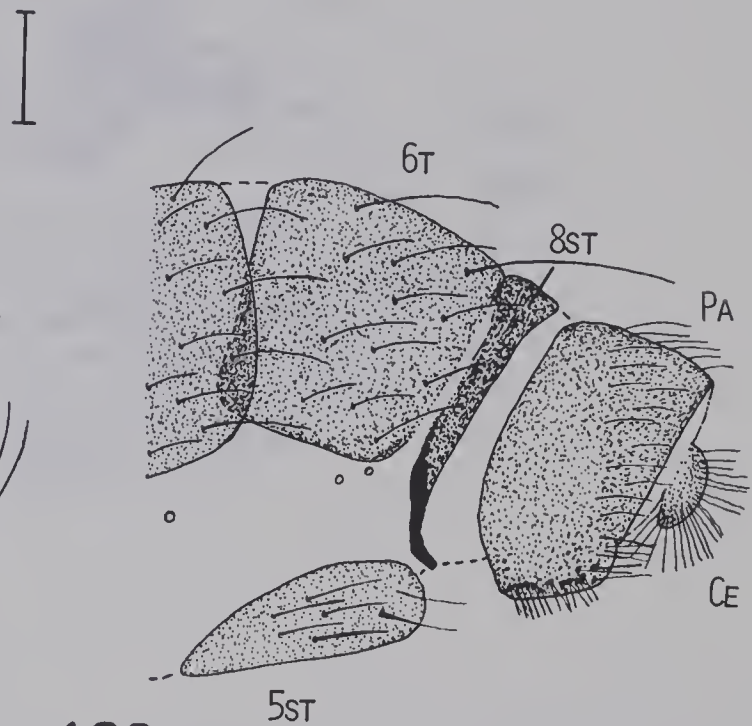
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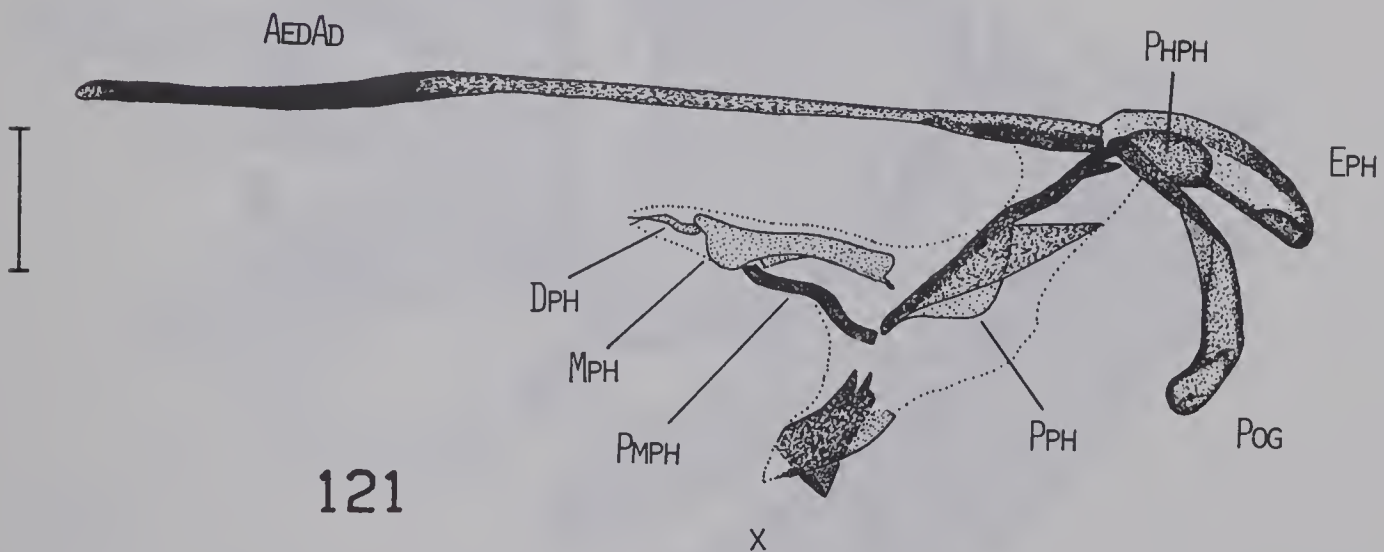
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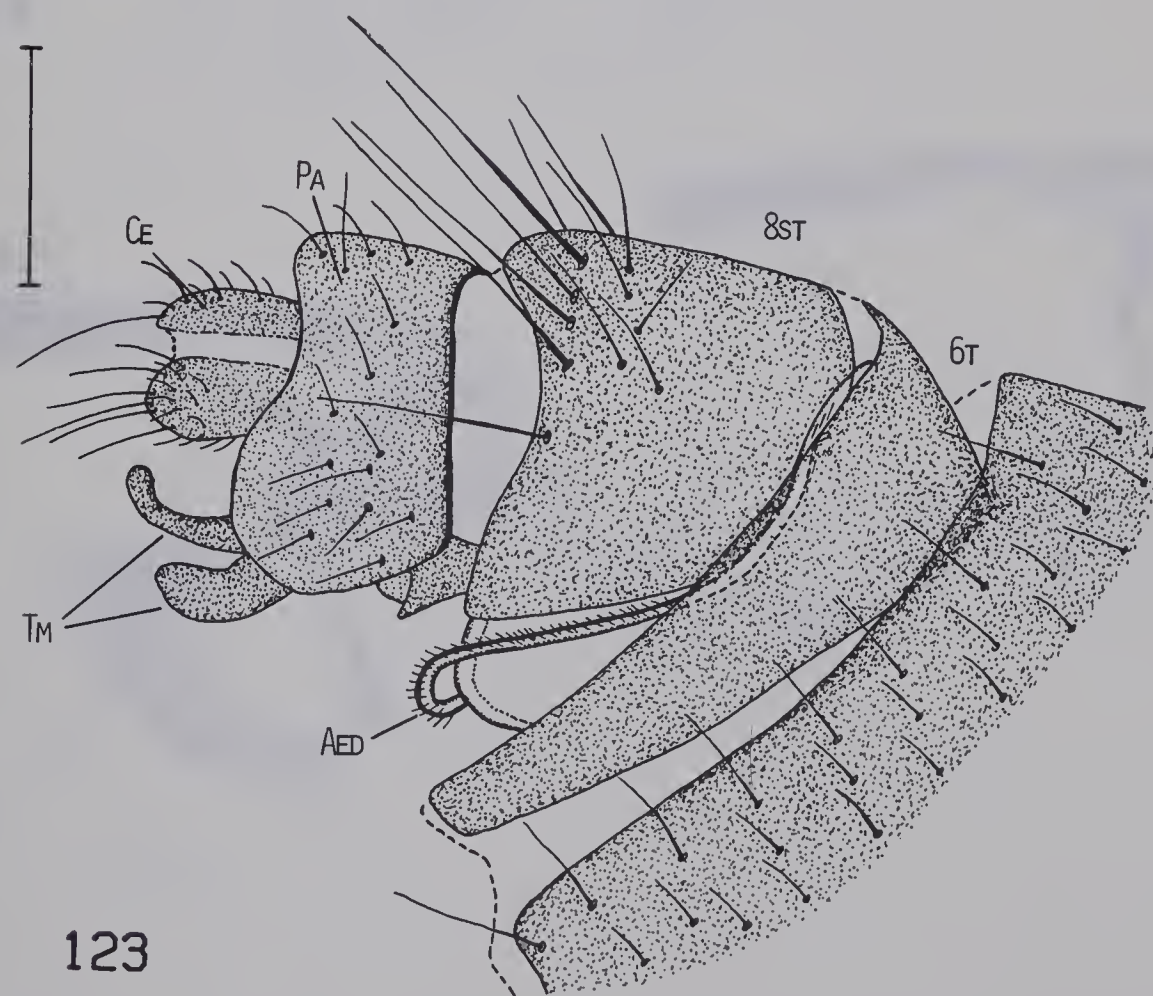
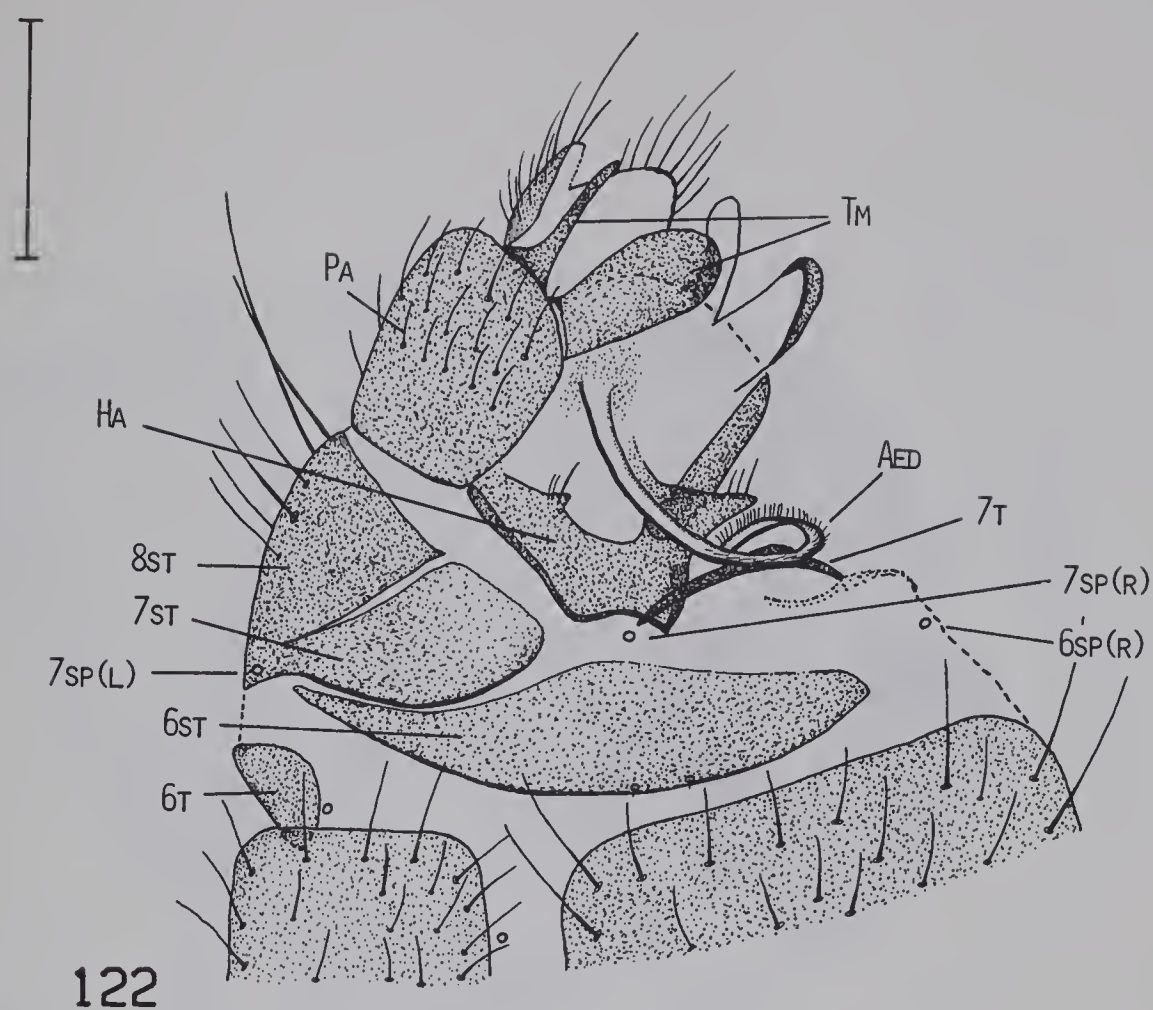
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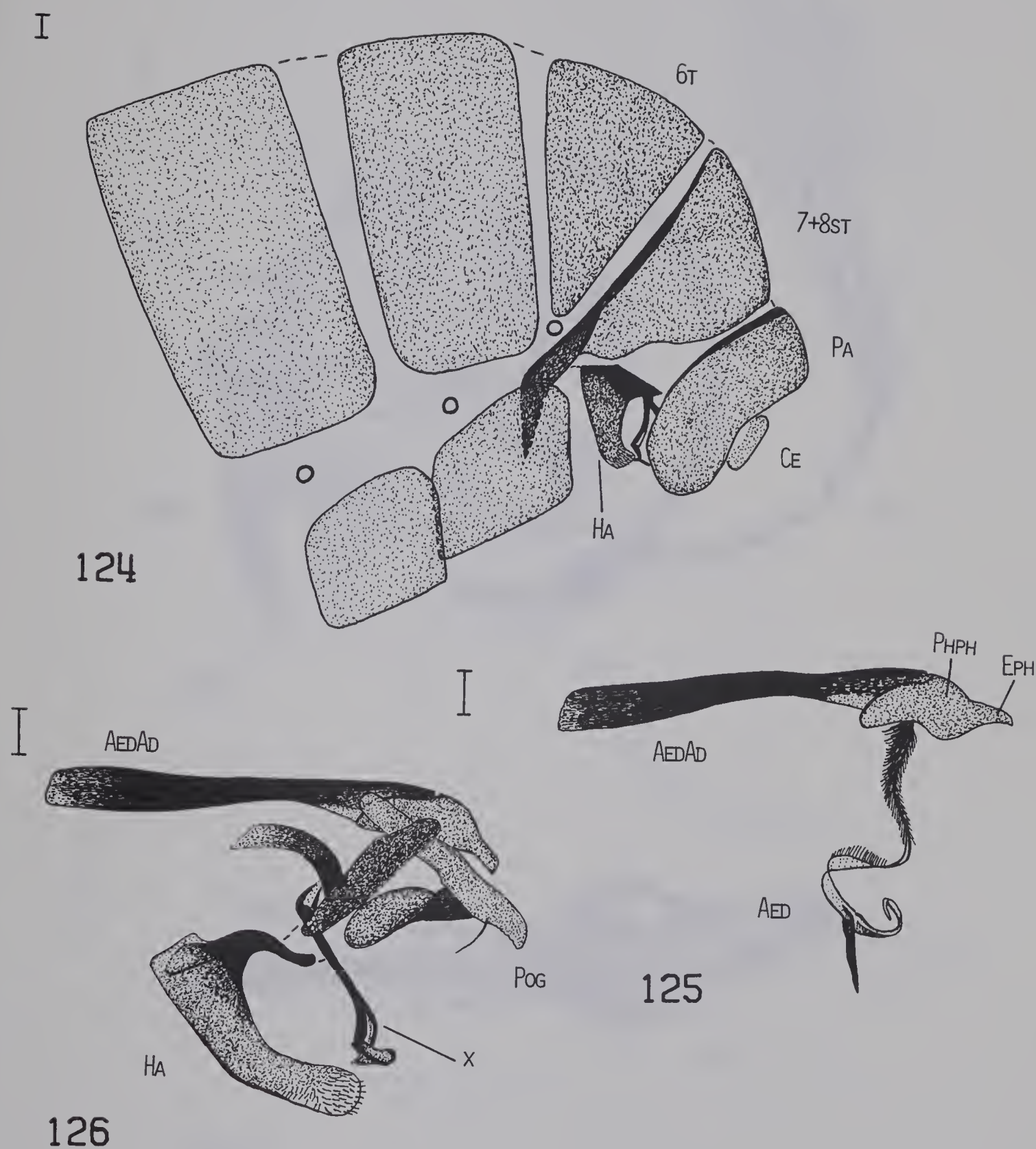
Figs. 118 - 121. 118. *Clusia lateralis* (Walker) (Clusiidae), aedeagus and associated structures (♂) in lateral view (with aedeagus in copulatory position). 119. *Clusia lateralis* (Walker) (Clusiidae), postabdomen (♂) in ventral view (with hypopygium removed). 120. *Phytomyza cineracea* Hendel (Agromyzidae), postabdomen (♂) in lateral view. 121. *Phytomyza symphyti* Hendel, aedeagus and associated structures (♂) in lateral view.

(Scale lines 0.1 mm.)



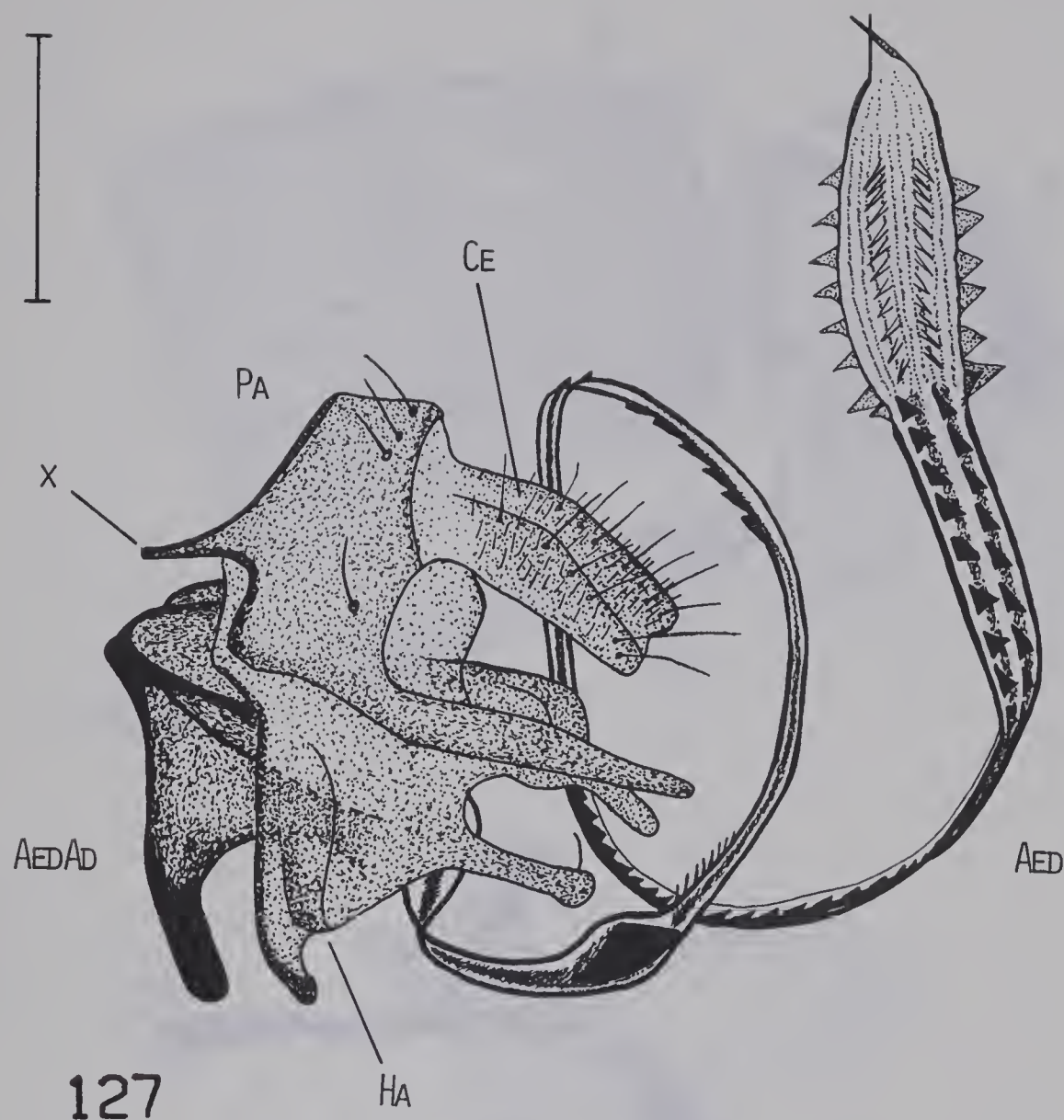
Figs. 122 - 123. 122. *Chiropteromyza wegeli* Frey (Chiropteromyzidae), postabdomen (♂) in ventral view. 123. *Chiropteromyza wegeli* Frey, postabdomen (♂) in dorsal view.

(Scale lines 0.1 mm.)



Figs. 124 - 126. 124. *Mormotomyia hirsuta* Austen (Mormotomyiidae), abdomen (part) (♂) in lateral view (with the dense pubescence omitted). 125. *Mormotomyia hirsuta* Austen, aedeagus and aedeagal apodeme (♂) in lateral view. 126. *Mormotomyia hirsuta* Austen, hypandrium, aedeagal apodeme and associated structures (♂) in lateral view.

(Scale lines 0.1 mm.)



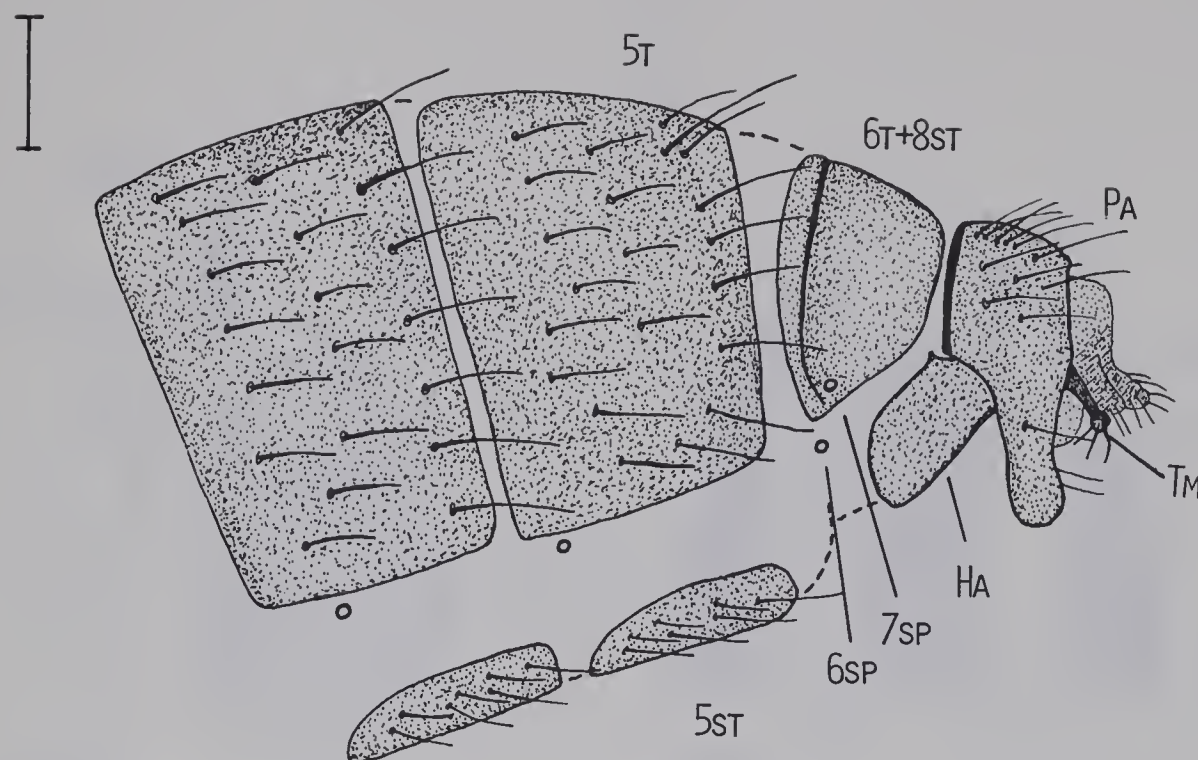
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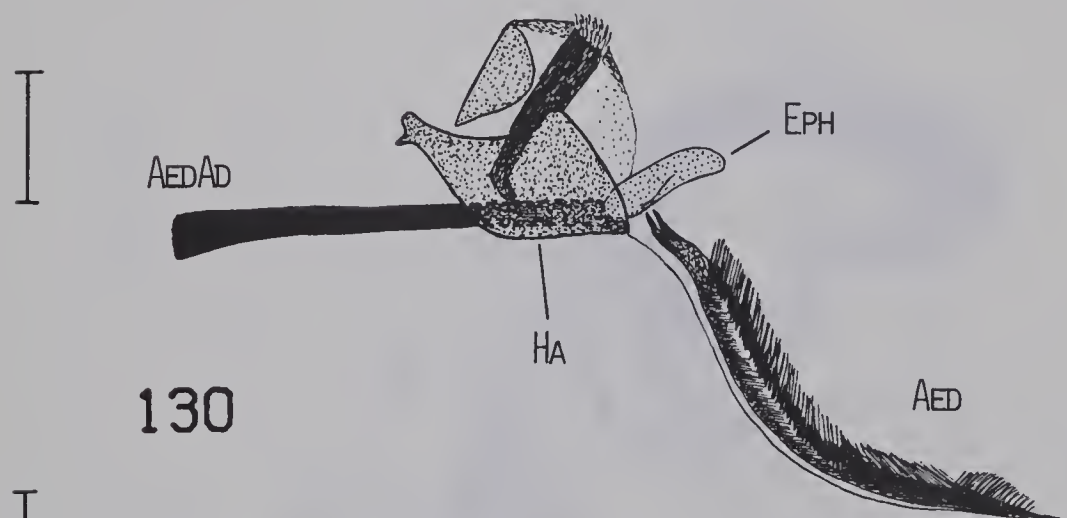
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Figs. 127 - 128. 127. *Prosopanthrum inerme* Malloch (Cnemospathidae), hypopygium (♂) in lateral view. 128. *Odinia boletina* (Zetterstedt) (Odiniidae), aedeagus, hypandrium and associated structures (♂) in ventral view (with aedeagus in copulatory position).

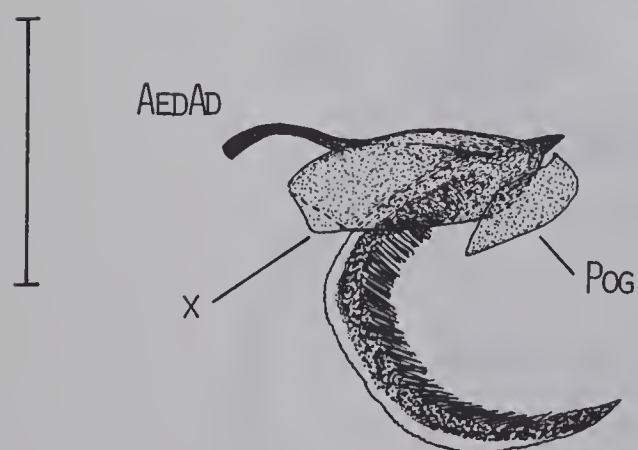
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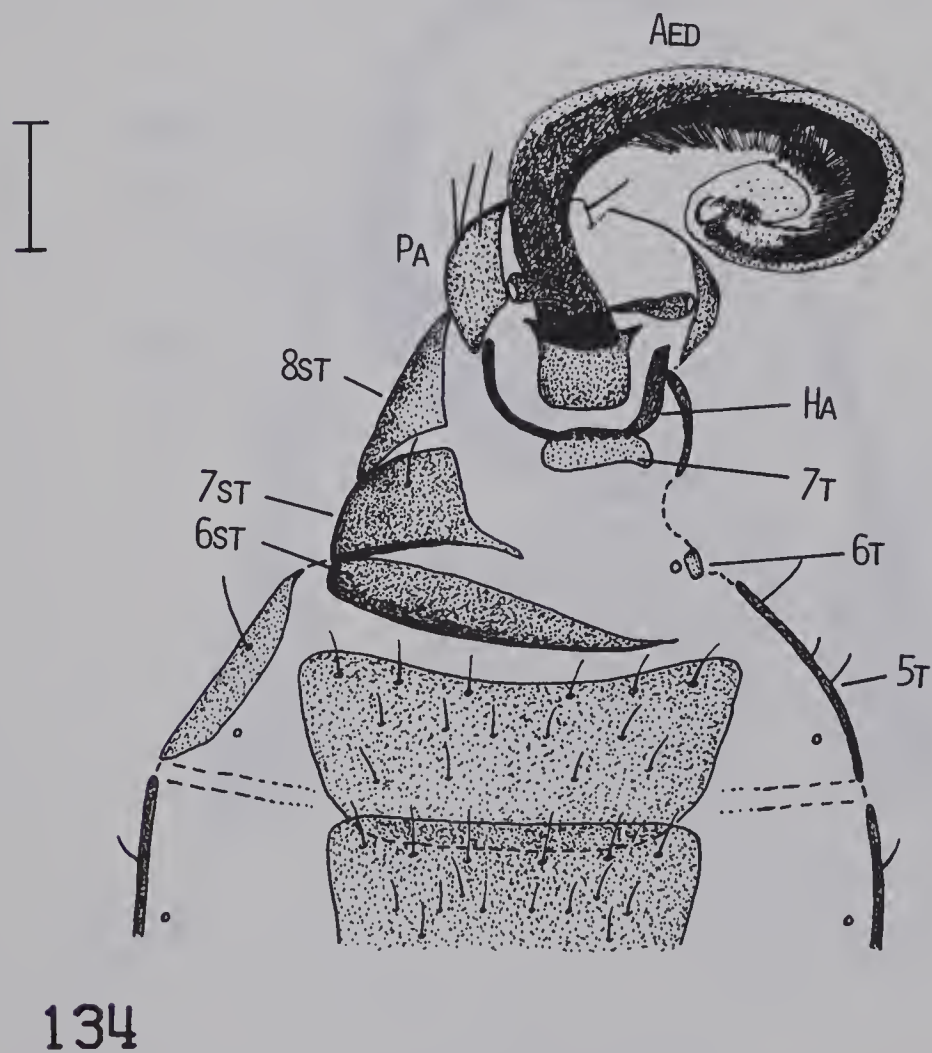
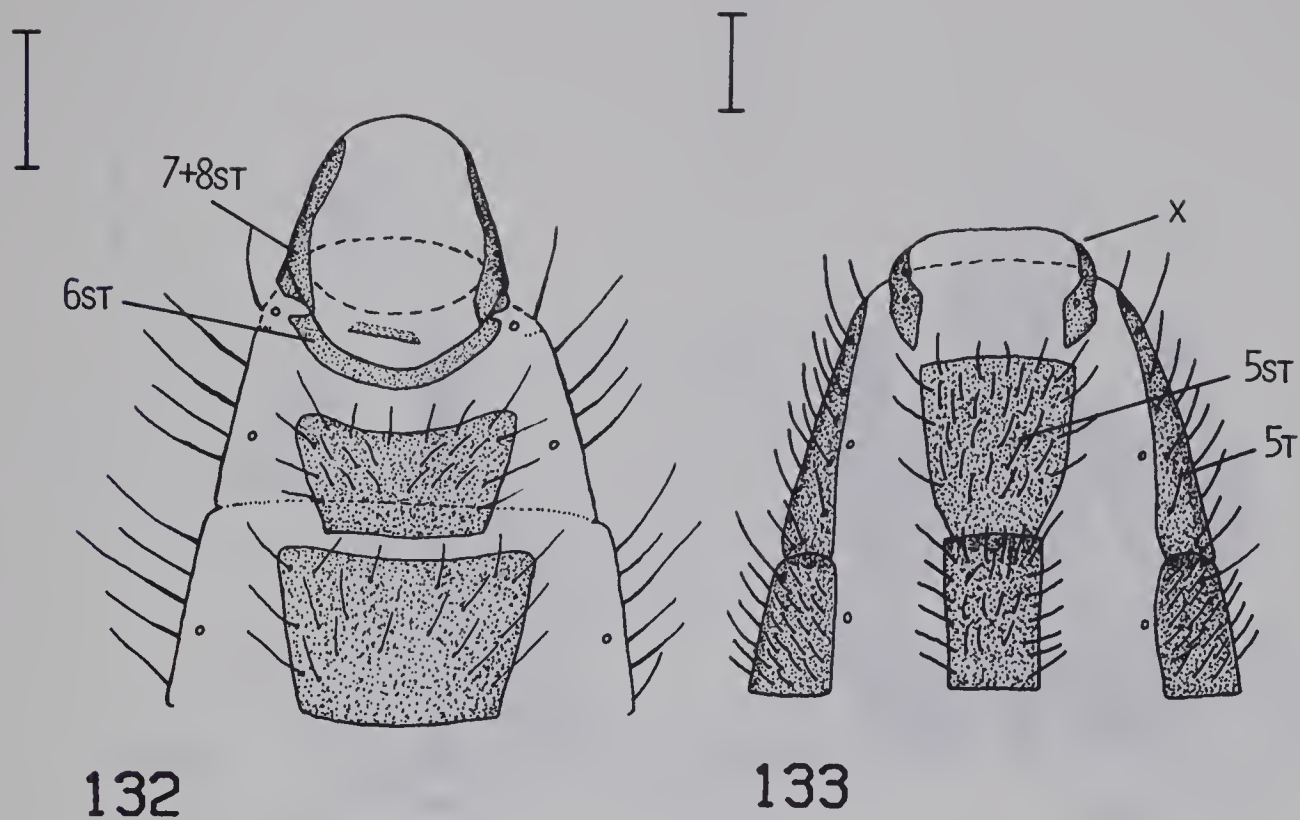
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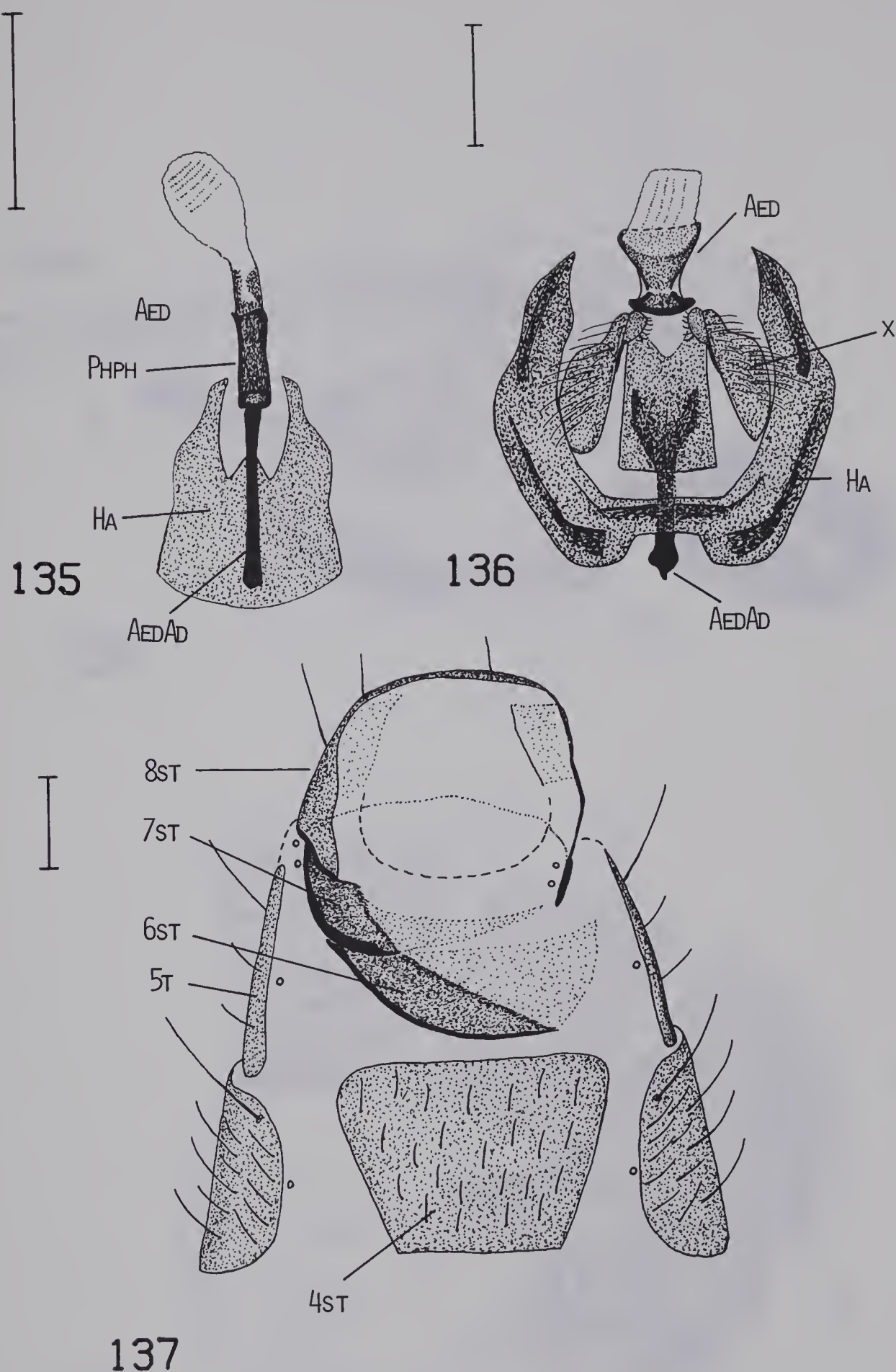
Figs. 129 - 131. 129. *Pelomyiella melanderi* (Sturtevant) (Tethinidae), abdomen (part) (♂) in lateral view. 130. *Pelomyiella melanderi* (Sturtevant), aedeagus, hypandrium and associated structures (♂) in lateral view. 131. *Acartophthalmus nigrinus* (Zetterstedt) (Acartophthalmidae), aedeagus and associated structures (♂) in lateral view.

(Scale lines 0.1 mm.)



Figs. 132 - 134. 132. *Acartophthalmus nigrinus* (Zetterstedt), abdomen (part) (♂) in ventral view (with hypopygium removed). 133. *Leptometopa latipes* (Meigen) (Milichiidae), abdomen (part) (♂) in ventral view (with hypopygium removed). 134. *Hemeromyia* sp. (Carnidae), abdomen (part) (♂) in ventral view.

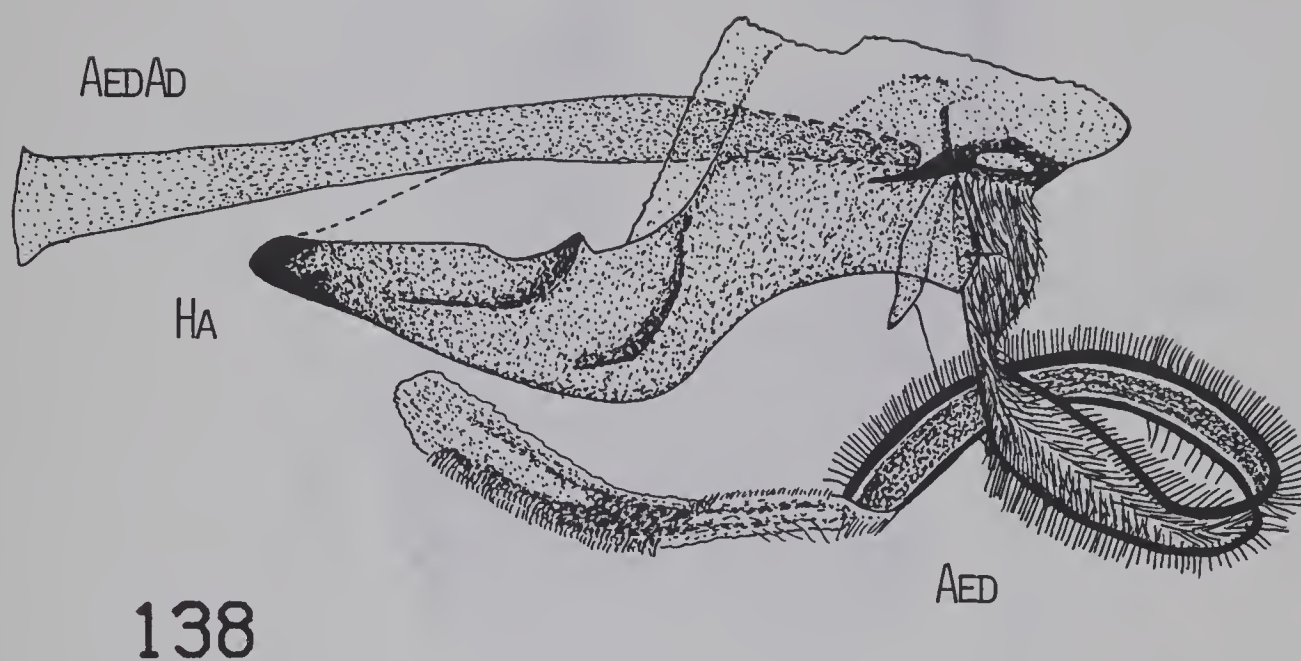
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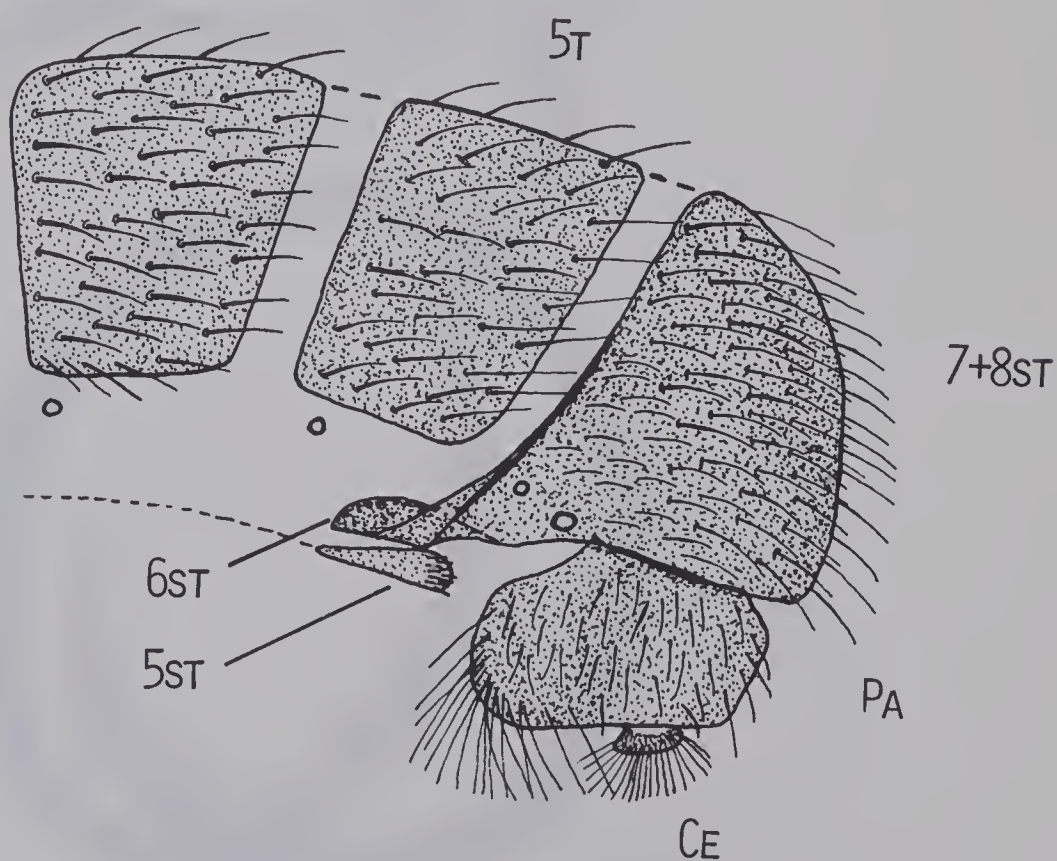
Figs. 135 - 137. 135. *Leptometopa latipes* (Meigen) (Milichiidae), aedeagus, hypandrium and associated structures (♂) in dorsal view. 136. *Lipara lucens* Meigen (Chloropidae), aedeagus, hypandrium and associated structures (♂) in ventral view. 137. *Lasiopleura shewelli* Sabrosky (Chloropidae), abdomen (part) (♂) in ventral view (with hypopygium removed).

(Scale lines 0.1 mm.)

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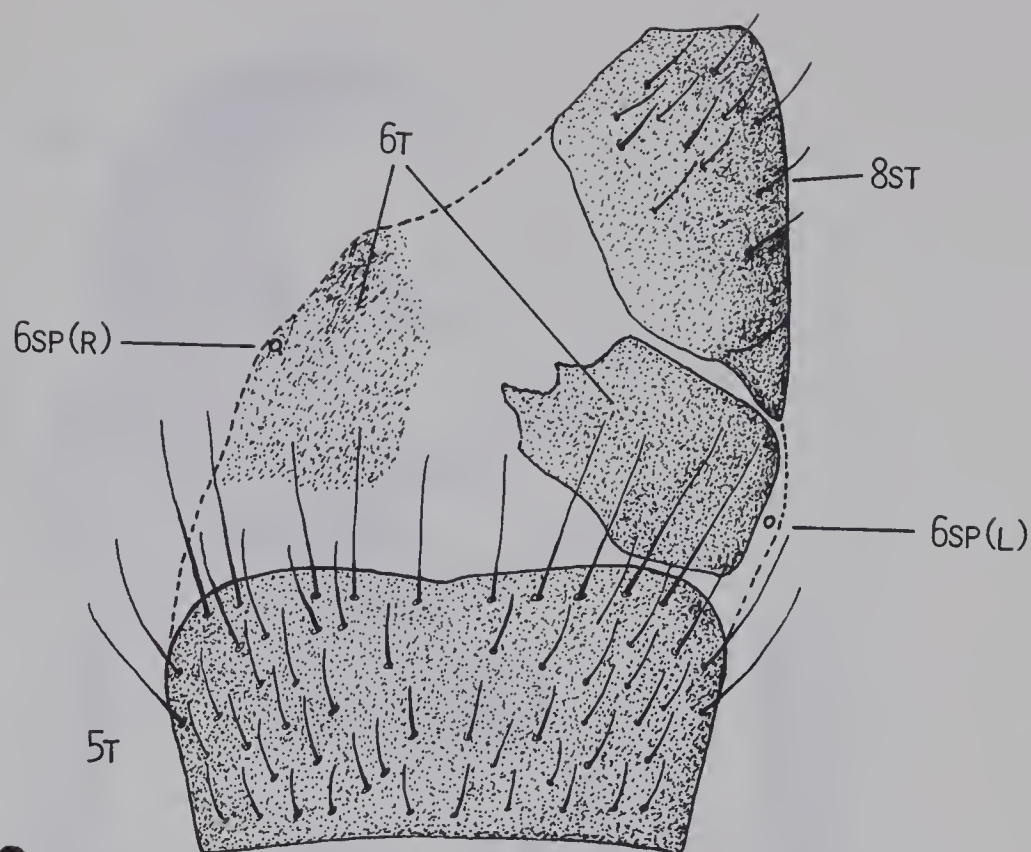
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Figs. 138 - 139. 138. *Dalmannia nigriceps* Loew (Conopidae), aedeagus, hypandrium and associated structures (♂) in lateral view. 139. *Zodion fulvifrons* Say (Conopidae), abdomen (part) (♂) in lateral view.

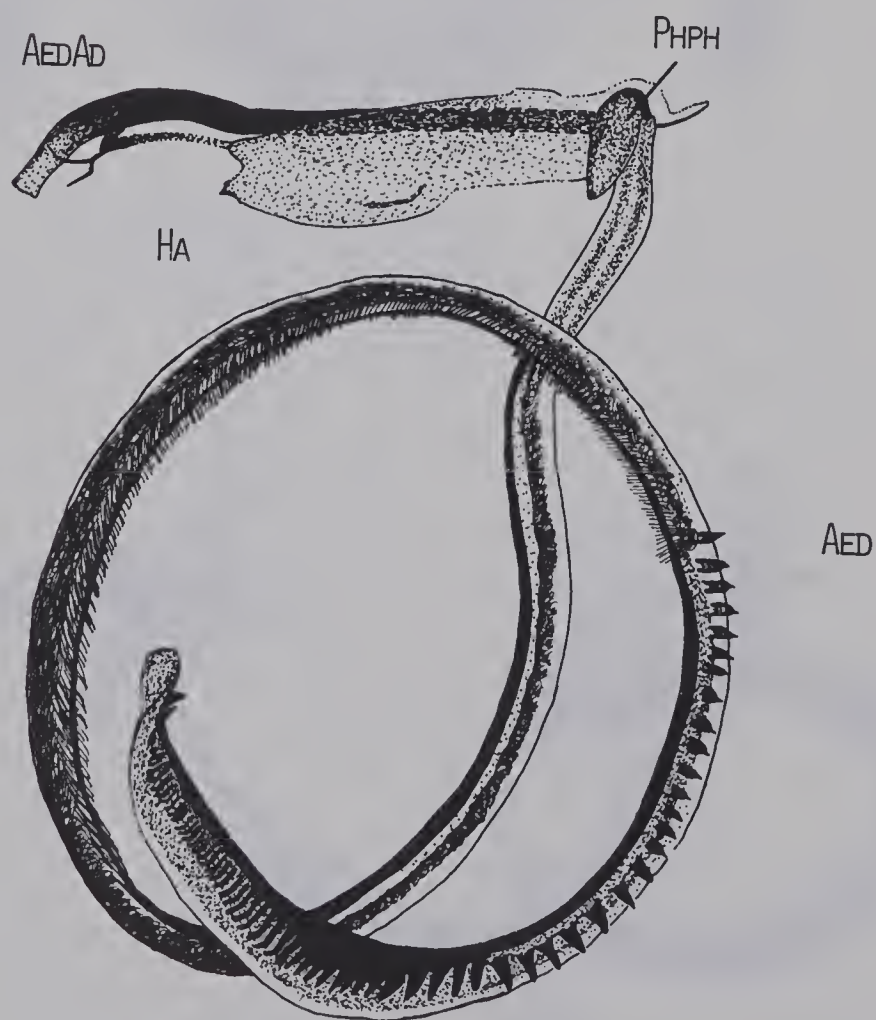
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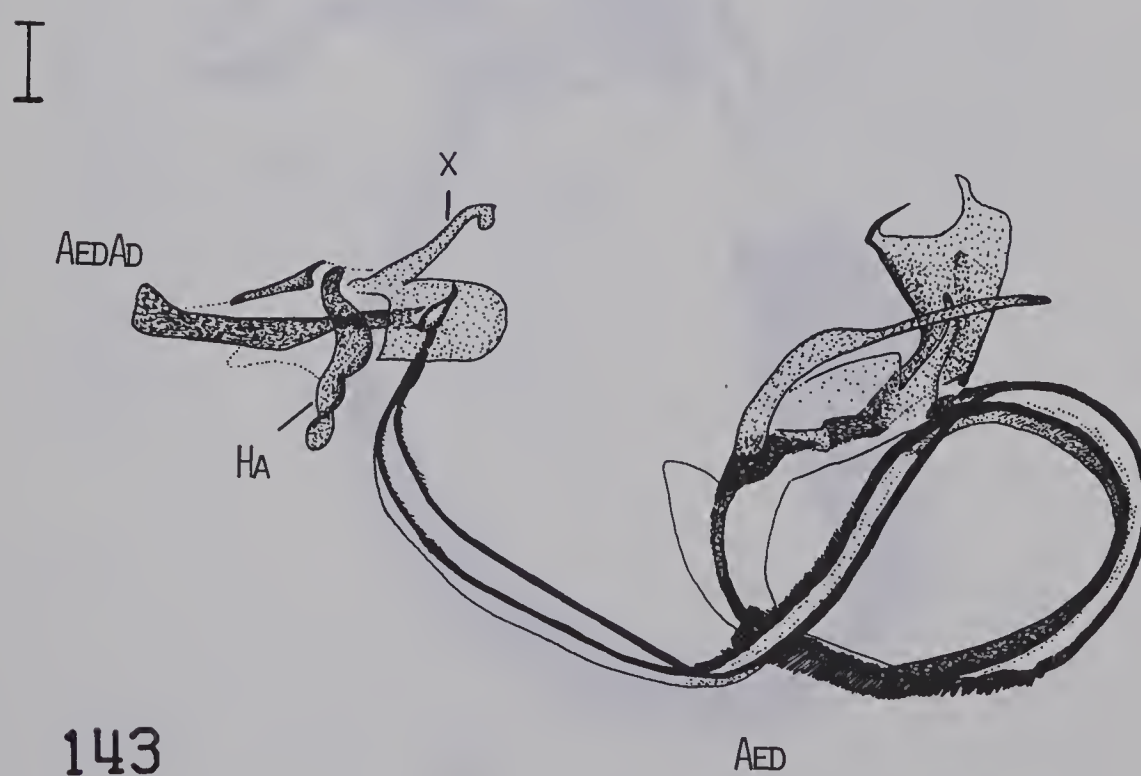
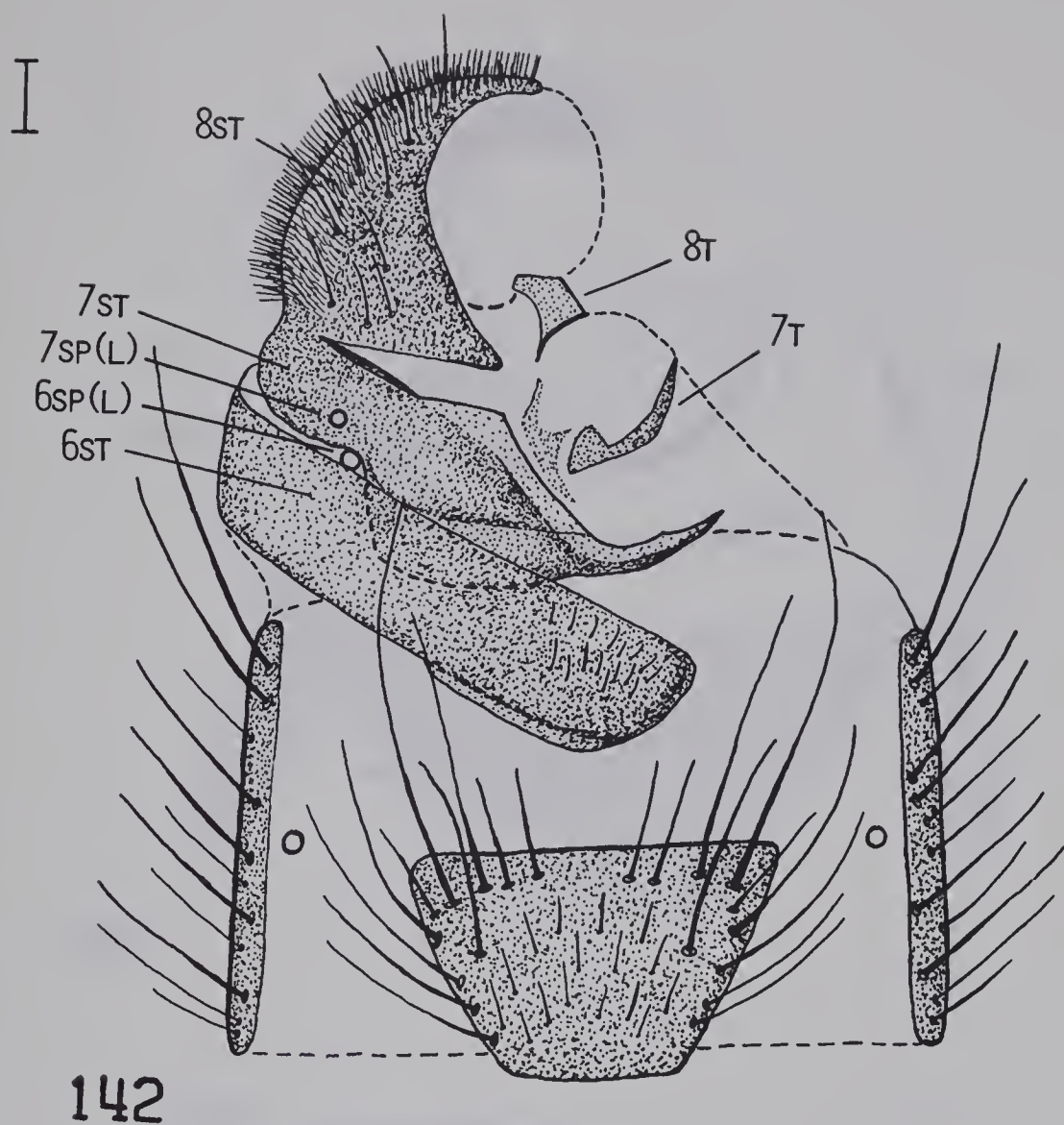
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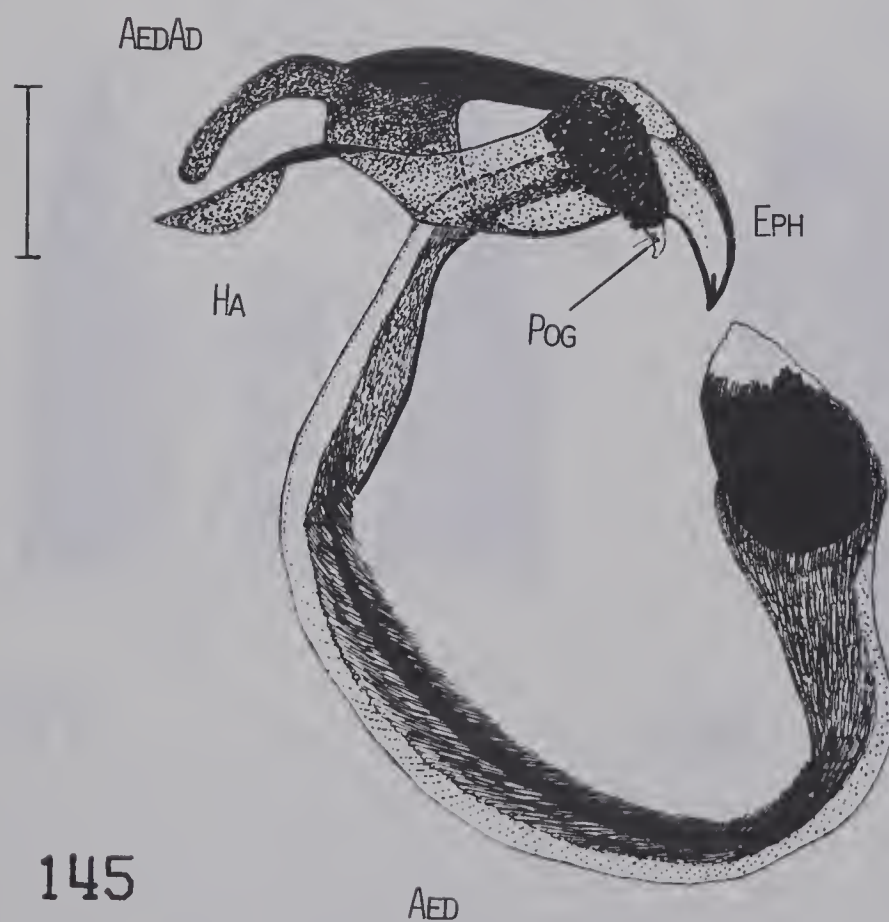
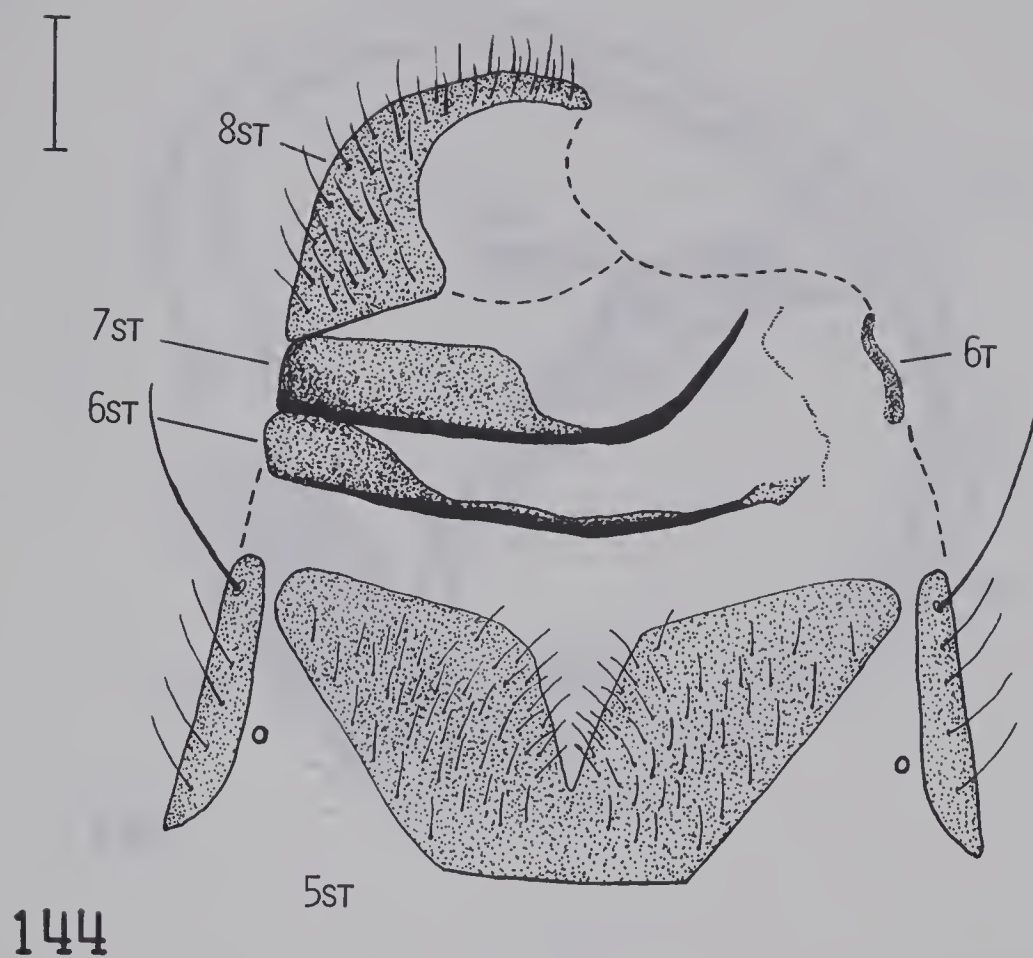
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Figs. 140 - 141. 140. *Eurygnathomyia bicolor* (Zetterstedt) (Eurygnathomyiidae), postabdomen (♂) in dorsal view (with hypopygium removed). 141. *Eurygnathomyia bicolor* (Zetterstedt), aedeagus, hypandrium and associated structures (♂) in lateral view.
(Scale lines 0.1 mm.)

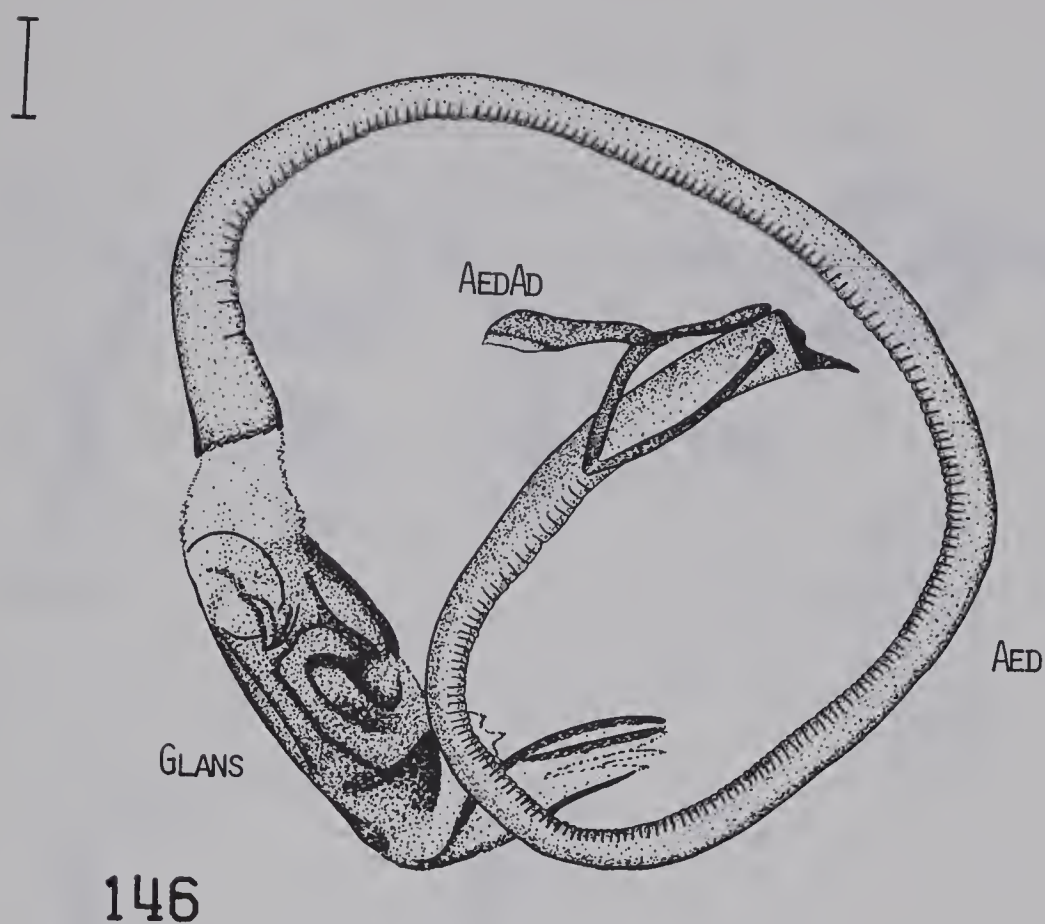


Figs. 142 - 143. 142. *Richardia* sp. (Richardiidae), postabdomen (♂) in ventral view (with hypopygium removed). 143. *Richardia* sp., aedeagus, hypandrium and associated structures (♂) in lateral view.

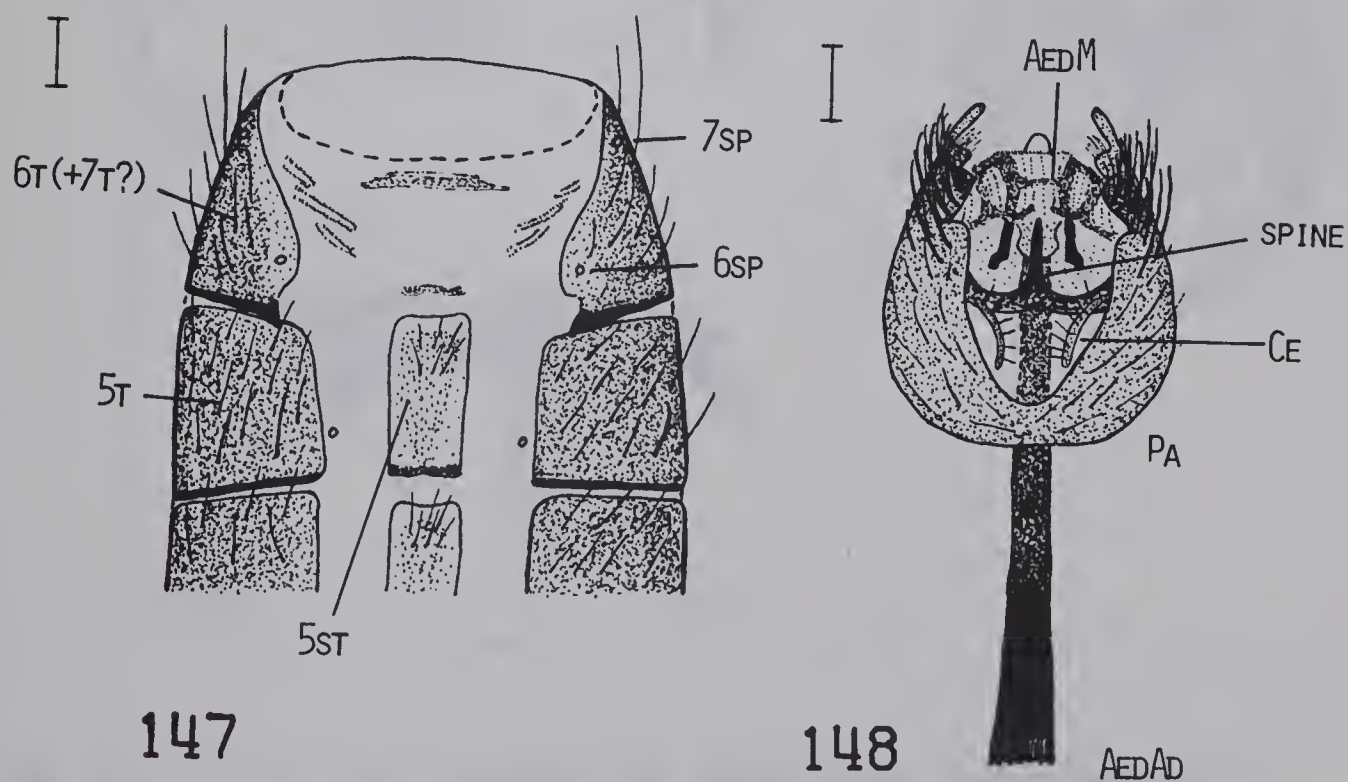
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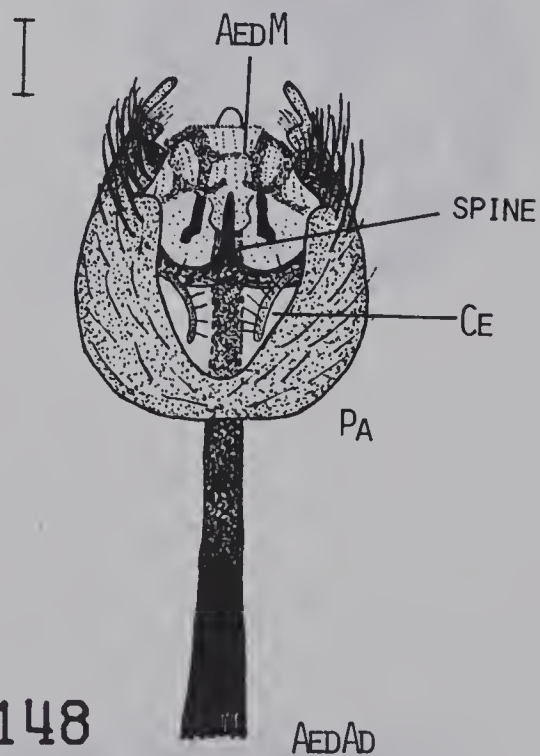
Figs. 144 - 145. 144. *Aenigmatomyia unipuncta* Malloch (see under Piophilidae s.l.), postabdomen (♂) in ventral view (with hypopygium removed). 145. *Aenigmatomyia unipuncta* Malloch, aedeagus, hypandrium and associated structures (♂) in lateral view.
(Scale lines 0.1 mm.)



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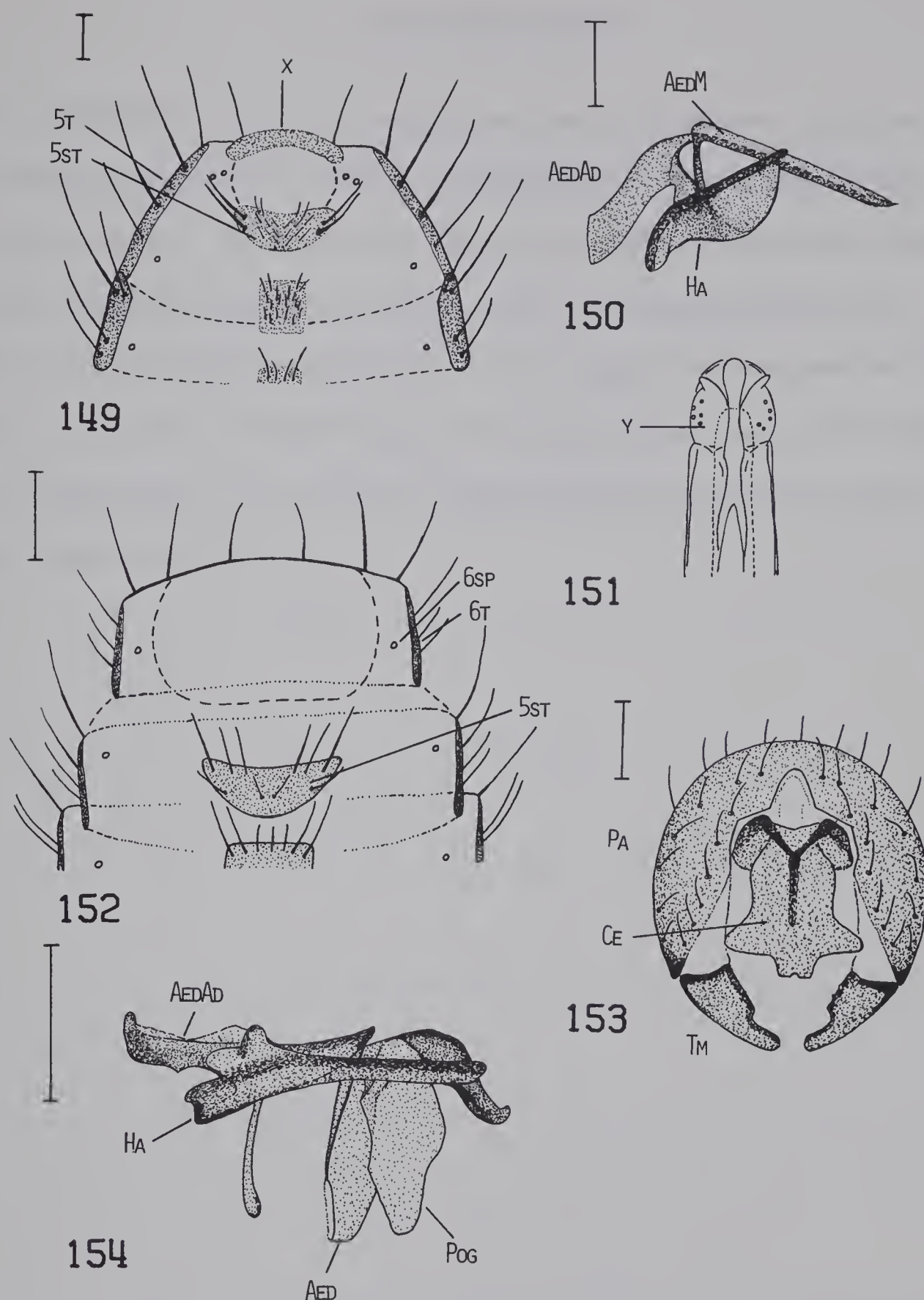
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Figs. 146 - 148. 146. *Orellia occidentalis* (Snow) (Tephritidae s.l.), aedeagus and aedeagal apodeme ("fultella") (♂) in lateral view. 147. *Canace snodgrassii* Coquillett (Canacidae), postabdomen (♂) in ventral view (with hypopygium removed). 148. *Canace snodgrassii* Coquillett, hypopygium (♂) in dorsal view.

(Scale lines 0.1 mm.)



Figs. 149 - 154. 149. *Fergusonina scutellata* (Fergusoninidae), abdomen (part) (♂) in ventral view (with hypopygium removed). 150. *Fergusonina scutellata* Malloch, aedeagus, hypandrium and associated structures (♂) in lateral view. 151. *Fergusonina evansi* Tonnoir, "tip of intromittent organ" (♂) in ventral view (after Tonnoir 1937). 152. *Notomyza edwardsi* Malloch (Notomyzidae), postabdomen (♂) in ventral view (with hypopygium removed). 153. *Notomyza edwardsi* Malloch, hypopygium (♂) in posterior view. 154. *Notomyza edwardsi* Malloch, aedeagus, hypandrium and associated structures (♂) in lateral view.

(Scale lines 0.1 mm.)

7. Concluding remarks

In conclusion, I wish to emphasize that phylogenetic systematics is a dynamic subject and that no classification system should ever be regarded as final. It is my hope that publication of this work will stimulate increased interest in this field and indicate where new research efforts might be directed. I also hope that my work will prove helpful to workers in other fields of biology, since one of the main aims of systematics is to provide classifications which are widely useful in many fields of research.

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APPENDIX 1. SOURCES OF INFORMATION ON MALE POSTABDOMEN OF SCHIZOPHORA

<u>Family</u>	<u>Important published sources of information</u>	<u>Species for which I have studied preparations</u>
Acartophthalmidae	Hennig (1938b)	<i>Acartophthalmus nigrinus</i> (Zetterstedt)
Agromyzidae	Speijer (1934), de Meijere (1938), Frick (1952), Nowakowski (1959, 1964), Ipe (1967)	many species in all major genera
Anthomyiidae	—	<i>Pegomya versicolor</i> (Meigen); <i>Hylemya (Delia) pilitaris</i> Stein; <i>Fucellia ariciiformis</i> (Holmgren)
Anthomyzidae	Hennig (1939a)	<i>Mimetopia occipitalis</i> Melander; <i>Anthomyza</i> sp. (also <i>Stenomiera</i> sp., doubtfully referred to this family)
Asteiidae	—	<i>Leiomyza laevigata</i> (Meigen); <i>Asteia amoena</i> Meigen
Aulacigastridae	Hennig (1969a)	<i>Aulacigaster leucopiza</i> (Meigen); <i>Cyamops nebulosus</i> Melander
Australimyziidae	—	<i>Australimyza anisotomae</i> Harrison
Borboropsidae	Hackman & Andersson (1969)	<i>Borboropsis puberula</i> (Zetterstedt)
Braulidae	Hennig (1938c, 1938d)	<i>Braula</i> sp.
Camillidae	—	<i>Camilla atripes</i> Duda
Campichoetidae	J.F. McAlpine (1962a)	<i>Campichoeta griseola</i> (Zetterstedt)
Canacidae	Wirth (1951)	<i>Canace snodgrassii</i> Coquillett; <i>Canaceoides</i> sp., <i>Xanthocanace nigrifrons</i> Malloch

(Cont'd)

<u>Family</u>	<u>Important published sources of information</u>	<u>Species for which I have studied preparations</u>
Carnidae	Hennig (1937b)	<i>Meoneura pteropleuralis</i> Sabrosky; <i>Meoneura flavifacies</i> Collin; <i>Hemeromyia</i> sp.
Chamaemyiidae	Hennig (1938e), J.F. McAlpine (1960)	<i>Chamaemyia juncorum</i> (Fallén); <i>Parochthiphila spectabilis</i> (Loew); <i>Acrometopia wahlbergi</i> (Zetterstedt)
Chiropteromyzidae	—	<i>Chiropteromyza wegelei</i> Frey
Chioropidae	—	<i>Rhodesiella subditea</i> Lamb; <i>Lipara lucens</i> Meigen; <i>Chlorops sulphureus</i> Loew; <i>Meromyza americana</i> Fitch; <i>Siphonellopsis lacteibasis</i> Strobl; <i>Lasiopleura shewelli</i> Sabrosky
Chyromyidae	—	<i>Chyromya flava</i> (L.); <i>Aphaniosoma oculicauda</i> Collin
Clusiidae	D.K. McAlpine (1960), Sasakawa (1966)	<i>Clusia lateralis</i> (Walker); <i>Clusiodes melanostoma</i> (Loew)
Cnemospathidae	Malloch (1933)	<i>Prosopanthrum inerme</i> Malloch
Coelopidae	Hennig (1937a), Steyskal (1957a, 1958b)	<i>Heterocheila hannai</i> (Cole); <i>Coelopa (Fucomyia) frigida</i> (F.); <i>Icaridion nasutum</i> Lamb; <i>Malacomyia sciomyzina</i> (Haliday)
Conopidae	Streiff (1906), Steyskal (1957a)	<i>Physocephala furcillata</i> (Williston); <i>Zodion fulvifrons</i> Say; <i>Thecophora modesta</i> (Williston); <i>Dalmannia nigriceps</i> Loew; <i>Stylogaster neglecta</i> Williston
Cremifaniidae	Delucchi & Pschorn-Walcher (1954), J.F. McAlpine (1963)	<i>Cremifania nigrocellulata</i> Czerny

(Cont'd)

<u>Family</u>	<u>Important published sources of information</u>	<u>Species for which I have studied preparations</u>
Cryptochetidae	Hennig (1937b)	<i>Cryptochetum nipponense</i> Tokunaga
Curtonotidae	Hackman (1960)	<i>Curtonotum helvum</i> (Loew)
Cypselosomatidae	D.K. McAlpine (1966), Hennig (1969a)	<i>Heloclusia imperfecta</i> Malloch; <i>Pseudopomyza atrimana</i> (Meigen); <i>Formicosepsis tinctipennis</i> de Meijere
Diopsidae	Hennig (1941a, 1941d)	<i>Centrioncus prodiopsis</i> Speiser; <i>Diopsis</i> sp.; <i>Sphyracephala brevicornis</i> (Say)
Drosophilidae	Salles (1948), Nater (1953), Laugé (1968), Gleichauf (1936), Hackman (1959), J.F. McAlpine (1968a)	<i>Drosophila busckii</i> Coquillett; <i>Drosophila</i> sp. cf. <i>melanogaster</i> Meigen (laboratory strain); <i>Amiota picta</i> (Coquillett)
Dryomyzidae	Hennig (1937a), Steyskal (1957b, 1958b)	<i>Dryomyza anilis</i> Fallén; <i>Helcomyza mirabilis</i> Melander; <i>Maorimyia bipunctata</i> (Hutton)
Ephydriidae	Clausen (1965), Bolwig (1940)	<i>Diastata vagans</i> Loew; <i>Hydrellia</i> sp.; <i>Psilopa</i> sp.
Eurychoromyiidae	J.F. McAlpine (1968b)	—
Eurygnathomyiidae	Morge (1967)	<i>Eurygnathomyia bicolor</i> (Zetterstedt)
Fanniidae	Chillcott (1960)	<i>Fannia canicularis</i> (L.)
Fergusoninidae	Tonnoir (1937)	<i>Fergusonina scutellata</i> Malloch
Glossinidae	Patton (1934), Zumpt (1936), Hennig (1937c)	<i>Glossina morsitans</i> Westwood

(Cont'd)

<u>Family</u>	<u>Important published sources of information</u>	<u>Species for which I have studied preparations</u>
Heleomyzidae	D.K. McAlpine (1967), Hennig (1969a)	<i>Fenwickia claripennis</i> Malloch; <i>Allophylopsis scutellata</i> (Hutton); <i>Orbellia tokyoensis</i> Czerny; <i>Heleomyza serrata</i> (L.); <i>Pseudoleria pectinata</i> (Loew); <i>Acantholeria armipes</i> (Loew); <i>Eccoptomera simplex</i> Coquillett; <i>Anorostoma marginatum</i> Loew; <i>Lutomyia hemiptera</i> (Curran); <i>Allophyla laevis</i> Loew; <i>Suillia plumata</i> (Loew)
Helosciomyzidae	Tonnoir & Malloch (1928)	<i>Helosciomyza subspiniocosta</i> Tonnoir & Malloch; <i>Huttonina abrupta</i> Tonnoir & Malloch
Heteromyzidae	—	<i>Tephrochlamys rufiventris</i> (Meigen); <i>Heteromyza atricornis</i> Meigen
Hippoboscidae (s.l.)	Theodor (1954a, 1954b, 1963), Theodor & Moscona (1954), Theodor & Oldroyd (1964), Jobling (1951), Zeve & Howell (1963).	—
Lauxaniidae	Hahn (1929), Hennig (1948a), Tenorio (1969)	<i>Celyphus obtectus</i> Dalman; <i>Camptoprosopeella borealis</i> Shewell; <i>Homoneura severini</i> Shewell; <i>Lauxania cylindricornis</i> (F.); <i>Meiosimyza platycephala</i> (Loew); <i>Minettia lupulina</i> (F.); <i>Lyciella annulata</i> (Melandar); <i>Lycia rorida</i> (Fallén); <i>Sapromyza cyclops</i> Melander; <i>Prorhaphochaeta imusta</i> (Meigen)
Lonchaeidae	J.F. McAlpine (1962b), Morge (1963)	<i>Dasiops passifloris</i> McAlpine; <i>Lonchaea polita</i> Say
Megamerinidae	Hennig (1941c)	<i>Megamerina dolium</i> (F.)

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<u>Family</u>	<u>Important published sources of information</u>	<u>Species for which I have studied preparations</u>
Micropezidae	Hennig (1934, 1936a)	<i>Calobata petronella</i> (L.); <i>Compsobata pallipes</i> (Say); <i>Compsobata univitta</i> (Walker); <i>Micropeza lineata</i> van Duzee; <i>Cnodacophora nasoni</i> (Cresson); <i>Taeniptera trivittata</i> Macquart
Milichiidae	Hennig (1937b, 1939a)	<i>Pholeomyia indecora</i> (Loew); <i>Leptomotopa latipes</i> (Meigen); <i>Milichia speciosa</i> Meigen; <i>Phyllomyza hirtipalpis</i> Malloch; <i>Desmometopa m-nigrum</i> (Zetterstedt)
Mormotomyiidae	Austen (1936), van Emden (1950), Hennig (in press)	<i>Mormotomyia hirsuta</i> Austen
Muscidae	Rivosecchi (1958), Hennig (1965a)	<i>Muscina assimilis</i> (Fallén); <i>Myospila mediatubunda</i> (F.); <i>Haematobia irritans</i> (L.)
Neriidae	—	<i>Gymnonerius fuscus ceylanicus</i> Hennig
Nothybidae	Aczél (1955)	<i>Nothybus longithorax</i> Rondani
Notomyzidae	Malloch (1933)	<i>Notomyza edwardsi</i> Malloch
Oдиниidae	Hennig (1938a, 1938e)	<i>Neoaalticomerus formosus</i> (Loew); <i>Odinia boletina</i> (Zetterstedt); <i>Odinia</i> sp.
Opomyzidae	Hennig (1939a), Vockeroth (1961)	<i>Opomyza germinationis</i> (L.); <i>Geomyza tripunctata</i> Fallén
Periscelididae	Hennig (1952b), Steyskal (1958a)	<i>Periscelis annulata</i> (Fallén); <i>Scutops maculipennis</i> Malloch; <i>Somatia</i> sp.

(Cont'd)

<u>Family</u>	<u>Important published sources of information</u>	<u>Species for which I have studied preparations</u>
Phaeomyiidae	—	<i>Pelidnoptera nigripennis</i> (F.)
Piophilidae (s.l.)	Hennig (1941a, 1943)	<i>Neottiophilum praeustum</i> (Meigen); <i>Centrophlebomyia furcata</i> F.; <i>Actenoptera hilarella</i> (Zetterstedt); <i>Piophila</i> (<i>Allopiophila</i>) <i>vulgaris</i> Fallén; <i>Piophila</i> (<i>Lasiopiophila</i>) <i>pilosa</i> Staeger; <i>Piophila</i> (<i>Prochyliza</i>) <i>xanthostoma</i> (Walker); (also <i>Heloparia bicolor</i> (Walker); <i>Aenigmatomyia unipuncta</i> Malloch and <i>Neomaorina bimacula</i> (Malloch) which are probably closely related to this family)
Psilidae	Hennig (1941b), Verbeke (1952)	<i>Psila rosae</i> (F.); <i>Psila fimetaria</i> (L.); <i>Loxocera cylindrica</i> Say; <i>Chyliza erudita</i> Melander
Rhinotoridae	Malloch (1933), Steyskal (1957a), D.K. McAlpine (1968)	<i>Anastomyza neglecta</i> Edwards; <i>Apophoneura inconspicua</i> Malloch; <i>Neorhinotora mutica</i> (Schiner); <i>Tapeigaster marginifrons</i> Bezzi
Richardiidae	Steyskal (1958c)	<i>Richardia</i> sp.; <i>Odontomera ferruginea</i> Macquart; <i>Epipleata erosa</i> Loew
Ropalomeridae	Steyskal (1957a), do Prado (1965)	<i>Rhytidops floridensis</i> (Aldrich)
Scatophagidae	—	<i>Cordilura</i> (<i>Cordilura</i>) <i>confusa</i> Loew; <i>Cordilura</i> (<i>Cordilura</i>) <i>latifrons</i> Loew; <i>Cordilura</i> (<i>Achaetella</i>) <i>varipes</i> (Walker); <i>Spaziphora cincta</i> (Loew); <i>Orthacheta cornuta</i> (Loew); <i>Pogonota gilvipes</i> (Loew); <i>Scatophaga aldrichi</i> (Malloch); <i>Scatophaga stercoraria</i> (L.); <i>Chylizosoma vittatum</i> (Meigen); <i>Hexamitocera vittata</i> Coquillett

(Cont'd)

<u>Family</u>	<u>Important published sources of information</u>	<u>Species for which I have studied preparations</u>
Sciomyzidae	Verbeke (1950)	<i>Pherbellia quadrata</i> Steyskal; <i>Pherbellia griseola</i> (Fallén); <i>Pherbellia albocostata</i> (Fallén); <i>Tetanura pallidiventris</i> (Fallén); <i>Sciomyza simplex</i> Fallén; <i>Pteromicra apicata</i> (Loew); <i>Elgiva sundewalli</i> Kloet & Hincks; <i>Tetanocera robusta</i> (Loew)
Sepsidae	Hennig (1937a, 1949)	<i>Orygma luctuosum</i> Meigen; <i>Nemopoda nitidula</i> (Fallén); <i>Sepsis vicaria</i> Walker; <i>Themira putris</i> (L.)
Sphaeroceridae	Hackman (1969), Richards (1961, 1968)	<i>Sphaerocera curvipes</i> Latreille; <i>Copromyza equina</i> Fallén; <i>Leptocera</i> sp.
Syringogastridae	do Prado (1969)	<i>Syringogaster rufa</i> Cresson
Tachinidae (s.l.)	Salzer (1968), Rohdendorf (1967), Verbeke (1963), Morrison (1941), Grunin (1964, 1966, 1969)	<i>Eucalliphora lilaea</i> (Walker); <i>Pollenia rudis</i> (F.); <i>Hypoderma lineatum</i> (Villers)
Tanypezidae	Hennig (1936b)	<i>Tanypeza luteipennis</i> Knab & Shannon; <i>Strongylophthalmyia</i> <i>angustipennis</i> Melander; <i>Neotanypeza elegans</i> (Wiedemann)
Tephritidae (s.l.)	Hennig (1936a, 1936c, 1939b, 1940, 1941a), Munro (1947), Rivosecchi (1957), Steyskal (1961), Morge (1967)	<i>Homalocephala similis</i> (Cresson); <i>Euxesta notata</i> (Wiedemann); <i>Physiphora demandata</i> (F.); <i>Chaetopsis massyla</i> (Walker); <i>Seioptera vibrans</i> (L.); <i>Pterocalla strigula</i> Loew; <i>Tetanops</i> sp.; <i>Otites stigma</i> (Hendel); <i>Melieria ochricornis</i> (Loew); <i>Platystoma seminationis</i> (F.); <i>Rivellia flavimana</i> Loew; <i>Senopterina foxleei</i> Shewell; <i>Pyrgota undata</i> Wiedemann; <i>Orellia occidentalis</i> (Snow); <i>Euxesta aequalis</i> (Loew); <i>Paroxyna murina</i> (Doane); <i>Epochra candensis</i> (Loew); <i>Palloptera</i> <i>trimaculata</i> (Meigen); <i>Palloptera superba</i> Loew

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APPENDIX 1 (Cont'd)

<u>Family</u>	<u>Important published sources of information</u>	<u>Species for which I have studied preparations</u>
Teratomyzidae	Vockeroth (in press)	<i>Teratomyza (sensu lato)</i> sp.
Tethinidae	Hennig (1939a, in press)	<i>Macrocanace littorea</i> (Hutton); <i>Tethina parvula</i> (Loew); <i>Pelomyiella melanderi</i> (Sturtevant)
Trixoscelididae	Hackman (1970)	<i>Trixoscelis</i> sp.

APPENDIX 2. ABBREVIATIONS USED ON PLATES AND FIGURES

AED	Aedeagus
AEDAd	Aedeagal apodeme
AEDM	Aedeagal mantle
BL	basal lobe of aedeagus
Bm	Basimere
CE	Cercus or cerci
DPH	Distiphallus
EA	Epandrium (9th abdominal tergum)
EJAP	Ejaculatory apodeme
EJB	Ejaculatory bulb
EJD	Ejaculatory duct
EPH	Epiphallus
HA	Hypandrium (9th abdominal sternum)
IM	Intermedium
MPH	Mesophallus
PA	Periandrium
PHPH	Phallophore
PL	Processus longus
PMPH	Paramesophallus
POG	Postgonite
PPH	Paraphallus
PRG	Pregonite
PRGSc	Pregenital sclerite
PROCT	Proctodaeum (hind gut)
PROCTG	Proctiger
RP	Rectal papilla
SET	Sensilla trichodea

T _M	Telomere
VA	vertical section of hypandrial arms
VP	ventral process of aedeagal apodeme
X, Y	other structures specified in the text
1 _{ST}	1st abdominal sternum
2 _{ST}	2nd abdominal sternum
4 _{SP}	4th abdominal spiracle
4 _T	4th abdominal tergum
5 _{SP}	5th abdominal spiracle
5 _{SP} (R)	5th abdominal spiracle (right side)
5 _{ST}	5th abdominal sternum
5 _T	5th abdominal tergum
6 _{PL}	6th pleural sclerite
6 _{SEG}	6th abdominal segment
6 _{SP}	6th abdominal spiracle
6 _{SP} (L)	6th abdominal spiracle (left side)
6 _{SP} (R)	6th abdominal spiracle (right side)
6 _{ST}	6th abdominal sternum
6 _T	6th abdominal tergum
7 _{SEG}	7th abdominal segment
7 _{SP}	7th abdominal spiracle
7 _{SP} (L)	7th abdominal spiracle (left side)
7 _{SP} (R)	7th abdominal spiracle (right side)
7 _{ST}	7th abdominal sternum
7 _T	7th abdominal tergum
8 _{ST}	8th abdominal sternum
8 _T	8th abdominal tergum
10 _T	10th abdominal tergum

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